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Evolution, ecology and systematics of symbiotic shrimps (Crustacea: Decapoda: Caridea)

Evoluce, ekologie a systematika symbiotických krevet (Crustacea: Decapoda: Caridea)

PhD THESIS

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Co-supervisor: prof. Zdeněk Ďuriš

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I declare that this thesis has not been submitted for the purpose of obtaining of the same or another academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

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ATTACHED PUBLICATIONS AND A MANUSCRIPT

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1. **Horká I.**, De Grave S., Fransen C.H.J.M., Petrusek A., Ďuriš Z., 2016. Multiple host switching events shape the evolution of symbiotic palaemonid shrimps (Crustacea: Decapoda). *Scientific Reports* 6: 26486.

2. **Horká I.**, De Grave S., Fransen C.H.J.M., Petrusek A., Ďuriš Z., Remarkable parallelism in evolution of the fish-cleaning phenomenon of anemone associated palaemonid shrimps. (manuscript)

3. Ďuriš Z., **Horká I.**, Juračka P. J., Petrusek A., Sandford F., 2011. These squatters are not innocent: The evidence of parasitism in sponge-inhabiting shrimps. *PLoS ONE* 6(7): e21987.

Part 2: Contributions to systematics of caridean shrimps

4. **Horká I.**, Fransen C.H.J.M., Ďuriš Z., 2016. Two new species of shrimp of the Indo-West Pacific genus *Hamodactylus* Holthuis, 1952 (Crustacea: Decapoda: Palaemonidae). *European Journal of Taxonomy* 118: 1–26.

5. Ďuriš Z., **Horká I**., 2016. *Salmoneus chadwickae*, a new alpheid shrimp (Crustacea: Decapoda: Alpheidae) from the Red Sea, with remarks on related or regional congeners. *Marine Biodiversity* 10.1007/s12526-015-0427-4.

6. **Horká I.**, De Grave S., Ďuriš Z., 2014. A new species of shrimp of the genus *Anachlorocurtis* Hayashi, 1975 from the Red Sea, with range extension of *A. commensalis* Hayashi, 1975 (Crustacea, Decapoda, Pandalidae). *Zookeys* 407: 9–28.

7. Ďuriš Z., **Horká I.**, Al-Horani F., 2011. *Periclimenaeus echinimanus* sp. nov. (Crustacea: Decapoda: Pontoniinae), a new species from the Gulf of Aqaba, Red Sea. *Zootaxa* 2983: 57–68.

8. Ďuriš Z., **Horká I.**, Sandford F., 2009. *Periclimenaeus pectinidactylus* n. sp. (Crustacea: Decapoda: Pontoniinae) from the Belizean Barrier Reef, Caribbean Sea. *Zootaxa* 2130: 31–40.

9. Ďuriš Z., **Horká I**., Hoc D.T., 2009. *Periclimenaeus nufu*, a new species of shrimp (Crustacea: Decapoda: Pontoniinae) from Vietnam. *Raffles Bulletin of Zoology* 57: 453–464.

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Abstract

This thesis is focused on symbiotic associations of caridean shrimps with a variety of marine animals of different phyla. Currently, five caridean families comprise symbiotic species. Palaemonidae (including the traditionally recognised subfamily Pontoniinae of predominantly symbiotic species) is the most species-rich and ecologically important of them. Its representatives live from temperate to tropical marine or brackish waters, with the highest diversity in the Indo-West Pacific biogeographic area and the western Atlantic.

The thesis is composed of two parts, one focusing on ecology and evolutionary biology, the other on systematics. The first part consists of three studies providing new knowledge on the evolution of symbioses in palaemonid shrimps. We confirmed that inter-phylum host-switching events and colonization of new hosts likely played a major role in the evolution of palaemonid symbiotic shrimps and these evolved multiple times (**Chapter 1**). Similarly, the switching from ecto- to endosymbiotic mode, associated with new body forms and ecological adaptations, occurred several times in palaemonid evolution. Reversal back to a free-living mode is rare, occasionally observed among ectosymbiotic lineages. Our results also confirm the necessity of systematic revision of this group, demonstrating that some of the wide-ranging taxa are polyphyletic. In the **Chapter 2**, we highlight a striking parallelism in evolution of unrelated phylogenetic lineages of fish-cleaning palaemonid shrimps from different biogeographical regions. Despite their morphology, colouration and behaviour via specific signals to fish clients are similar, minor but important distinctions may be observed in all those aspects. The **Chapter 3** is focused on elucidation of relation among sponge-associated shrimps and their hosts. We proved a parasitic character of trophic relation in sponge-associated shrimps. Based on detailed morphology using the scanning electron microscopy, we documented that their shear-like claws show evidence of intensive shearing of host tissues and, according to analyses of stomach contents, we demonstrate feeding on host tissues.

The second part includes descriptions of seven new species of caridean shrimps. Majority of them comprise symbiotic species of Palaemonidae (5 spp.), Pandalidae (1 sp.), and Alpheidae (1 sp.). Two new coral-associated species of the palaemonid genus *Hamodactylus* (*H. paraqabai*, *H. pseudaqabai*) are described based on specimens from Papua New Guinea, the Great Barrier Reef, Indonesia and Malaysia (**Chapter 4**). Their systematic position is confirmed by molecular analyses. The new alpheid shrimp, *Salmoneus chadwickae*, from the Red Sea (**Chapter 5**) was probably associated with burrowing animals. It belongs to the *S. cristatus* species group and it is distinguishable from all congeners by morphology as well as molecular data. The **Chapter 6** contains description of a new antipatharian-associated pandalid shrimp *Anachlorocurtis occidentalis* from the Red Sea. Morphological differences and molecular analysis supported its separation from *A. commensalis* from the north western Pacific. Finally, three new sponge-associated shrimps of *Periclimenaeus* were described based on morphological features (**Chapters 7-9**); two species from the Indo-West Pacific region (*P. echinimanus* and *P. nufu*), and one from the Caribbean Sea (*P. pectinidactylus*).

Abstrakt (in Czech)

Disertační práce je zaměřena na symbiotické vztahy krevet z infrařádu Caridea se zástupci z různých kmenů bezobratlých. V současné době je v rámci Caridea známo pět čeledí se symbiotickými druhy. Ekologický významná a druhově nejpočetnější je čeleď Palaemonidae, která podle tradičního pojetí zahrnuje i podčeleď Pontoniinae s většinou symbiotických druhů. Její zástupce můžeme nalézt ve slaných a brakických vodách, od mírného pásu po pás tropický, s nejvyšší druhovou diverzitou v Indo-západotichomořské geografické oblasti a západním Atlantiku.

Disertační práce je rozdělena na dvě části, ekologicko-evoluční a systematickou. Ekologická část přináší nové poznatky o evoluci symbiotických vazeb u krevet z čeledi Palaemonidae. V **Kapitole 1** jsme potvrdili, že kolonizace nového hostitele, mnohdy z jiného kmene, se u symbiotických krevet této skupiny v průběhu evoluce vyskytuje opakovaně a sehrává významnou roli při její diverzifikaci. Stejně tak přechod z ektosymbiotického způsobu života na endosymbiotický, spojený se vznikem adaptací souvisejících s celkovým tvarem těla, se v evoluci Palaemonidae objevuje opakovaně. Návrat k volnému způsobu života je vzácný a vyskytuje se výjimečně u fylogenetických linií s ektosymbiotickými zástupci. Výsledky fylogenetické analýzy mimo jiné ukázaly na polyfylii u několika rodů a nutnost hlubší systematické revize celé čeledi. V **Kapitole 2** jsme prokázali s využitím fylogenetických analýz nápadný paralelismus u dvou nepříbuzných a geograficky vzdálených linií krevet „čističů“. Ačkoli jsou tyto krevety velmi podobné z hlediska morfologie, zbarvení a specifických prvků chování, vyskytují se zde nepatrné, ale významné odlišnosti. **Kapitola 3** se zabývá určením povahy vztahu mezi krevetami a jejich hostiteli, mořskými houbami. U spongobiontních krevet jsme prokázali, že se vůči svým hostitelům chovají jako parazité. S využitím elektronové skenovací mikroskopie jsme zdokumentovali, že klepeta spongobiontních krevet mají typický tvar nůžek, a nesou stopy po intenzivním „stříhání“ hostitelských tkání. Analýza obsahu jejich žaludků zároveň potvrdila přítomnost sponginu a skleritů hostitele.

Druhá část disertační práce zahrnuje popisy sedmi nových druhů krevet (Caridea). Většinu z nich tvoří symbiotické druhy čeledi Palaemonidae (5 dr.), další nové taxony jsou z čeledi Pandalidae (1 dr.) a Alpheidae (1 dr.). **Kapitola 4** zahrnuje popisy dvou nových krevet rodu *Hamodactylus* (*H. paraqabai*, *H. pseudaqabai*) z čeledi Palaemonidae, které žijí v symbióze s „měkkými“ koráli (laločníky řádu Alcyonacea). Vzorky byly získány z Papuy Nové Guiney, Velkého bariérového útesu, Indonésie a Malajsie. Systematická pozice obou druhů byla potvrzena s využitím molekulárních znaků. Nový druh krevety z čeledi Alpheidae, *Salmoneus chadwickae* z Rudého moře (**Kapitola 5**), je pravděpodobně vázán na některé živočichy vyhrabávající si na dně norky. Kreveta *S. chadwickae* patří do skupiny druhů *S. cristatus*, její odlišnost od ostatních druhů byla potvrzena na základě morfologie i molekulárních znaků. **Kapitola 6** zahrnuje popis nového druhu krevety *Anachlorocurtis occidentalis* (Pandalidae) z Rudého moře, která žije v symbiotickém vztahu s černými korály řádu Antipatharia. Morfologické rozdíly i molekulární analýza potvrdily vyčlenění nového druhu od zástupce *A. commensalis* ze severozápadního Pacifiku.

Kapitoly 7-9 zahrnují tři nové spongobiontní krevety rodu *Periclimenaeus* popsané na základě morfologických znaků. Dva druhy (*P. echinimanus* a *P. nufu*) pocházejí z Indo-západotichomořské oblasti. Jeden druh (*P. pectinidactylus*) je popsán z Karibského moře.

Outline of publications and a manuscript

This thesis consists of two parts focusing on 1) ecology and phylogeny of caridean shrimps, and 2) systematics of this group. The subject linking the both parts is the shrimp symbiosis, mainly in representatives of Palaemonidae.

The main topics of the first, ecological and evolutionary, part are the phenomena of host-switching in the evolution of symbioses, the cleaning symbiosis, and the nature of associations in sponge-dwelling palaemonid shrimps; two studies from this part were published by the present author as the first- or second-authored papers in international peer-reviewed journals (**Chapters 1, 3**). Another first-authored study, focusing on fish-cleaner palaemonids (**Chapter 2**), is presented as a manuscript that will be submitted to a peer-reviewed journal later.

The family Palaemonidae is known as the most speciose family of the caridean shrimps primarily occurring in tropical and subtropical shallow-water benthic habitats, with their highest marine diversity in the Indo-West Pacific area. Many members of this group live in symbioses with other marine invertebrates, this symbiotic life causing high host specificity followed by various morphological adaptations and types of coexistence.

In the **Chapter 1**, we aim to understand, using molecular data, the evolutionary history of symbiotic lifestyles in palaemonid shrimps. Compared with other recent similar studies, our phylogenetic analyses include representatives from main centres of palaemonid speciation (Indo-West Pacific and tropical western Atlantic) as well as from some other regions. We performed analyses based on four and three genes (mitochondrial and nuclear ones), covering 87 and 107 species belonging to 43 and 48 genera, respectively. Together with free-living species, representatives of taxa associated with sponges, cnidarians, molluscs, echinoderms and ascidians were investigated. Based on analysed material, we indicated seven main clades within Palaemonidae, in all but one at least some symbiotic members were represented (with the exception of the clade containing hymenocerids and gnathophyllids represented here by two free-living species). Most free-living taxa were nested predominantly in the most basal clade. Based on the ancestral state reconstruction of host associations, we confirmed that (1) symbiotic forms evolved multiple times from free-living species, primarily into cnidarian ectosymbioses, and that (2) reversal back to the free-living mode of life is a rare phenomenon. We also demonstrated that (3) switching from ecto- to endosymbiotic modes of life also occurred multiple times, resulting in species-specific associations with bivalve molluscs, sponges and ascidians, which led to development of morphological, colour and behavioural adaptations in shrimps. The present phylogenetic analysis also clearly confirmed (4) the polyphylies or paraphylies of several palaemonid genera, such as *Ancylomenes*, *Cuapetes*, *Periclimenes* or *Zenopontonia*, and highlighted the necessity of their systematic revision.

The **Chapter 2** explores the interspecific symbiotic relation between palaemonid shrimps and fishes. In this association which generally is regarded as mutualistic, the shrimps play the role of cleaners and fishes the role of their clients. We used DNA analysis to reconstruct the phylogeny of Palaemonidae based on a selection of 70 species representing all major symbiotic and free-living assemblages, but focusing widely to cnidarian symbioses; 14 species there belong to palaemonid cleaner shrimps. All known palaemonid genera containing fish-cleaners were represented, i.e., *Ancylomenes*, *Periclimenes*, *Brachycarpus*, *Palaemon* and *Urocaridella*. The molecular data confirmed at least five independent origins of the fish-cleaning symbioses within this family. This study discusses their multiple evolutions expressed in morphological, colour and behavioural parallelisms suggesting similarities in communication of the cleaners with fish clients.

Two geographically separated and evolutionary divergent lineages of true fish-cleaning shrimps, the Indo-West Pacific *Ancylomenes* spp., and the western Atlantic *Ancylomenes*/*Periclimenes* spp., evolved independently from anemone-associated forms. These groups are very similar in following

aspects: (1) in general shape of body and colour pattern; (2) use of anemones as well-recognizable cleaning stations; (3) displaying a side-way body swaying to visualise brightly coloured abdomen attracting fishes; (4) further communication with client-fish (with the vigorous cheliped clapping being documented only in Indo-West Pacific species). This apparent phenotypic convergence is so striking that one of the Atlantic taxa was assigned to the newly erected genus *Ancylomenes* together with unrelated Indo-West Pacific (IWP) taxa.

The remaining three evolutionarily more basal lineages are represented by the Indo-West Pacific genus *Urocaridella*, the pantropic/temperate *Brachycarpus biunguiculatus*, and with the Atlantic species *Palaemon elegans*. Most aspects mentioned above, except of use of anemones as cleaning station, are presented in *Urocaridella* spp. (which usually occur in groups in their cleaning station in reef crevices). In *B. biunguiculatus* and two *Palaemon* species, which are only occasionally observed as fish cleaners, the general morphology and colouration are different from the abovementioned palaemonid cleaners, and the claw signalling or side-way body swaying has not been reported.

Chapter 3 contributes to the knowledge on some aspects of associations between sponge-dwelling shrimps and their hosts. Marine sponges belong to the hosts frequently inhabited by small crustaceans including palaemonid and alpheid shrimps. Our research of Caribbean sponge-dwelling shrimps based on examinations of their stomach contents and some morphological aspects suggests that sponge-inhabiting shrimps are often parasites adapted to consumption of host sponge tissues. Microscopic analysis revealed the presence of a large number of spicules or spongin threads in stomach contents of shrimps, and confirmed that the host tissue is the major source of food for shrimp genera *Onycocaris*, *Periclimenaeus*, *Thaumastocaris*, *Typton* (all Palaemonidae), and *Synalpheus* (Alpheidae). We also found that sponge-associated shrimps showed interesting morphological adaptations to the parasitic feeding on host tissues. Their chelae showed specific shape similar to scissors or garden shears. The use of scanning electron microscopy revealed the traces of intensive shearing in claws of *Typton carneus*, which confirmed their purpose for cutting the host tissue. Published morphological data show similar shear-like claw and/or mouthpart morphology also in other sponge-associated species from Palaemonidae (e.g., *Epipontonia*, *Poripontonia*, *Typtonychus*, *Onycocaridella* and *Onycocaris*), or Disciadidae (*Discias*). Also the mouthpart adaptations in examined species (reduction of incisor or molar processes) supported specialization for feeding on sponge tissue. Reduction of the mandibles was documented also in other sponge-associated taxa, including newly described *Periclimenaeus* species (**Chapter 8**), in contrast with the robust mandibular processes known in the majority of free-living caridean shrimps. Based on these characteristics and stomach content analyses, we assume that feeding parasitism is apparently widely distributed among spongobiotic shrimps. However, it is possible that under some conditions the pair of shrimps can offer certain benefits to their host as a defence towards other potentially harmful invaders, and this profit finally may outweigh losses caused by the shrimp feeding. My contribution in this second-author study included sampling and laboratory works during an expedition to the Caribbean Sea, participation in determination, and providing feedback during preparation of this manuscript.

The second part of my PhD thesis deals with the caridean shrimp taxonomy and comprises selected descriptions of new species belonging to three families (Palaemonidae – 5 species, Alpheidae – 1 species, Pandalidae – 1 species). With the exception of two, they represent obligatory symbiotic forms (**Chapters 4-9**). This part of the thesis includes two first-authored, and four second-authored papers in peer-reviewed international journals. My contribution in the second-author studies included field and laboratory works during expeditions focused on shrimp diversity in the Red Sea, the South China Sea, and the Caribbean Sea, participation in shrimp identifications, molecular analyses and

processing of data to obtain phylogenetic results (in the Chapter 5), assistance in preparation of illustrations, and revisions of draft texts of the manuscripts.

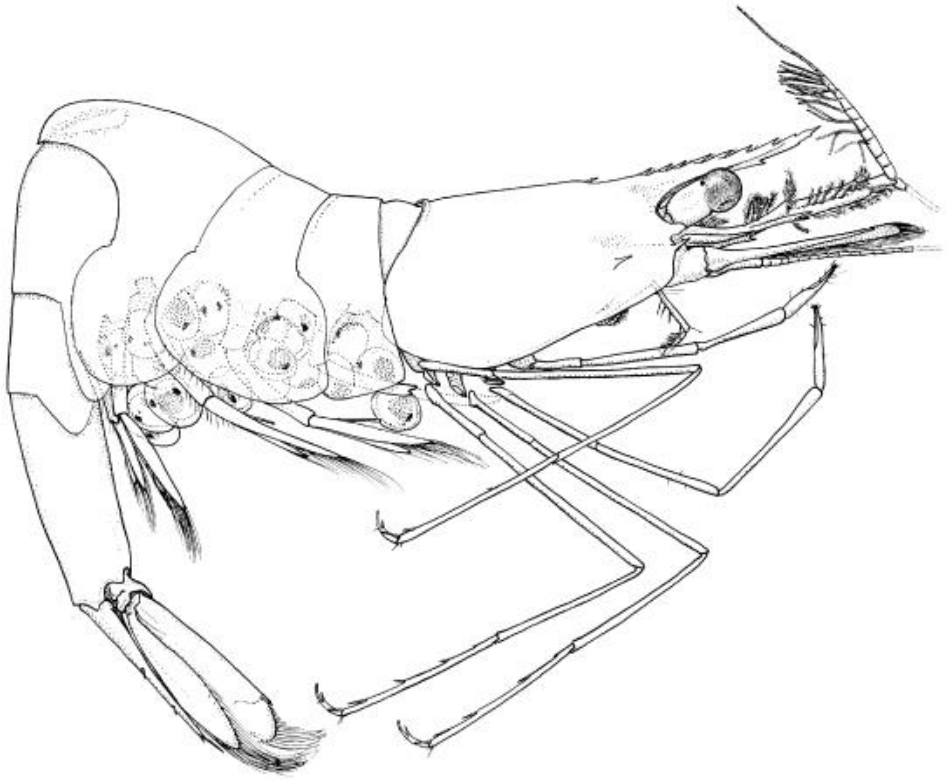
The **Chapter 4** includes the descriptions of two new alcyonacean-associated IWP palaemonid shrimps of the genus *Hamodactylus* which comprised four species up to now. The genus is unique among symbiotic palaemonid shrimps in the strong reduction in size of the second pereiopods, up to small and slender appendages similar to the ambulatory legs. All members of this genus are symbionts of soft or hard corals. The new species *Hamodactylus paraqabai* from Papua New Guinea and the Great Barrier Reef, and *H. pseudaqabai* from Indonesia and Malaysia, were distinguished based on morphological and molecular divergences from related *H. aqabai* from the Red Sea. The main distinguishing morphological feature from the other congeners is the presence of multiple teeth distally on the cutting edges on fingers of the first pereiopods. Both further differ in a level of the reduction of the fixed finger on the second pereiopods. In conformity with morphological divergence, both new species were well supported also in phylogenetic and haplotype network analyses of the mitochondrial gene for cytochrome c oxidase subunit I (COI).

The new species *Salmoneus chadwickae* (Alpheidae) was collected in the Gulf of Aqaba, northeastern Red Sea, during my research fellowship in the Marine Science Station in Aqaba, Jordan (**Chapter 5**). This brightly yellow-coloured shrimp was found in sandy bottom under stones with *Acropora* corals. Although symbiotic relation of this species remains unknown, other congeners live in burrows together with their hosts, the 'mud shrimps' (previous Thalassinidea). This species is the fifth member of the *Salmoneus cristatus* species group. Based on phylogenetic analysis of the mitochondrial (16S rRNA) and the nuclear (Histone 3) genes, it is closely related to *S. cristatus*. Morphologically it is distinguishable from all congeners by a strongly hooked, right-angled tip of the fixed finger on the major chela. More than 40 *Salmoneus* species are known at the present, but we can assume that future molecular revision might discover a wider series of cryptic taxa within this genus.

The next new species described from the Red Sea is symbiotic pandalid shrimp *Anachlorocurtis occidentalis* (**Chapter 6**) associated with antipatharian corals. The symbiotic associations with other animals are rare within Pandalidae and only three species with highly modified body shape and colouration were documented at present. All are small, slender, and compressed shrimps with a cryptic colour pattern matching their host. Our morphological studies using the scanning electron microscopy and COI-based molecular analysis well support the sister position of the new species *A. occidentalis* to the only known congener, *A. commensalis*; the latter was previously known only from Japan, and recently we documented it also from Taiwan. The morphological distinctions between both species include differences, e.g., in length of propodi and dactyli of the 3^{rd}-5^{th} pereiopods, in hooked dorsal lobe on the carapace, in the shape of eyes, or in the length of the 6^{th} abdominal segments.

Standard systematic descriptions of three new palaemonid species based on morphological features are presented in **Chapters 7-9**. All these species are representatives of the genus *Periclimenaeus* (with around 70 actually known species) which includes mainly symbiotic members associated with sponges or compound ascidians. The first new species, *P. echinimanus* (**Chapter 7**), named for erected spinules covering the chelae of the second pereiopods, was found in the Gulf of Aqaba (northeastern Red Sea). This species is placed in the *P. robustus* species-group, and closely related to *P. rhodope* with granulated (not spinulose) chelae. The second new species, the Caribbean species *P. pectinidactylus* (**Chapter 8**) was named to reflect the unique shape of the cutting edges of the first pereiopod fingers. According to several morphological features, the new species appears being closely related to *Holthuisaeus bermudensis*. Due to lack of the major cheliped in the only known specimen, the holotype, the systematic relation of the new species to *Holthuisaeus* remains unknown.

And finally, the third species of *Periclimenaeus*, *P. nufu* (**Chapter 9**), was found in Vietnamese waters during a joint Vietnamese-Norwegian project NUFU in the South China Sea. This species belongs to the *P. robustus* species group and is well distinguishable from most *Periclimenaeus* species, among others also by a unique shape of the widely ovate uropodal exopods, by produced distolateral lobe on the first pereiopod coxa, and articulated anteroventral angle of the carapace. Unfortunately, the only specimen was collected from rubble of dead corals and no host was detected. Considering that many encrusting and boring sponges are often present on dead corals, it may be supposed that this species is a symbiont of sponges.



Leptomenaeus nhatrangensis Ďuriš & Horká, 2008

1. General introduction to symbiotic shrimps

The term symbiosis (derived from Greek σύν=with, βίωσις=life) to indicating 'living together', was originally used in 1879 by the German scientist Heinrich Anton de Barry, who defined it as the relationship of "any two organisms living in close association, commonly one living in or on the body of the others" (see Rohde 2005). According to this, the general term symbiosis covers wide range of symbiotic relations. The basic types of symbiotic relations and their definitions by Rohde (2005) are as follows: *Mutualism* – both organisms derive a benefit but the association is not obligatory (e.g., cleaner shrimps, section 4.6; **Chapter 2**); *Commensalism* – organism collects food from the internal or external environment of a host without affecting the host in any way; *Parasitism* – association of two organisms in which one (parasite) benefits at the expense of the other (host) (e.g., sponge-dwelling shrimps in **Chapter 3**). Some authors consider symbiosis and mutualism as synonyms (Gunn and Pitt 2012). For the purpose of this thesis, the term *symbiosis* is interpreted in its wider definition, as equivalent to the term *association*; the symbiotic shrimps regularly reported as living on surface of their host are regarded *ectosymbionts* and shrimps living most of their life inside the host body (e.g., in mantle cavity of bivalve-molluscs, branchial cavity of ascidians, sponge channels and oscula) are reported here as *endosymbionts*.

In many cases, the nature of symbiotic relations among shrimps and their hosts is feebly investigated, or unknown. Earlier authors generally used for describing associations among shrimps and their hosts the term "*commensalism*", considering that shrimps evidently live on/in their hosts, but the true trophic and other relations between the partners remained often unknown (Bruce 1976b). Only a few studies of stomach or gut contents or morphological adaptations suggest that shrimps feeding on mucus or detritus from the surface of the host are true commensals (e.g., Johnson 1967; Johnson and Liang 1966), while other studies suggest that the shrimp/host relationship tends to be closer to parasitism (e.g., Bruce and Svoboda 1983; Fautin et al. 1995; **Chapter 3**). In fact, interactions between shrimps and their hosts most likely represent complex of various relationships (Chadwick et al. 2008; **Chapter 3)**.

The symbiotic associations between shrimps and other marine animals are characteristic especially for the caridean shrimps, the second most species-rich group within Decapoda (De Grave and Fransen 2011; De Grave et al. 2015). The symbiotic shrimps are reported in five presently recognized caridean families, i.e., Palaemonidae (with the traditional subfamilies Palaemoninae and Pontoniinae; **Chapters 1, 3, 4, 7, 8**), Alpheidae (**Chapter 5**), Pandalidae (**Chapter 6**), Thoridae, and Lysmatidae (e.g., Bruce 1976a,b). I introduce all of them below.

The Palaemoninae and Pontoniinae have recently been formally synonymised with Palaemonidae by De Grave et al. (2015). The actual subdivision of this family still remains unresolved. I started to work on this thesis before these systematic changes were suggested, and included published papers are primarily focused on the symbiotic shrimps of Palaemonidae which were traditionally placed within Pontoniinae. For the purpose of this thesis, I thus refer to such shrimps under their traditional name (i.e., 'pontoniine shrimps'). The shrimps of the previously recognized families Gnathophyllidae and Hymenoceridae are regarded here as inner lineages of the 'pontoniine shrimps', as already confirmed by recent DNA analyses (Mitsuhashi et al. 2007; Gan et al. 2015; De Grave et al. 2015; **Chapter 1**).

In general, when applying systematic classification of the caridean shrimp families including symbiotic representatives (below), I follow De Grave and Fransen (2011) and De Grave et al. (2014); the names and authorities for higher taxa (suborder and infraorders) have been specified by Poore (2016):

Crustacea: Malacostraca
Order Decapoda Latreille, 1802
Suborder Pleocyemata Burkenroad, 1963
Infraorder Caridea Latreille, 1817
Superfamily Palaemonoidea Rafinesque, 1815
Family Palaemonidae Rafinesque, 1815
Subfamily Palaemoninae Rafinesque, 1815
Subfamily Pontoniinae Kingsley, 1879
Superfamily Alpheoidea Rafinesque, 1815
Family Alpheidae Rafinesque, 1815
Family Thoridae Kingsley, 1879
Family Lysmatidae Dana, 1852
Superfamily Pandaloidea Haworth, 1825
Family Pandalidae Haworth, 1825

1.1 Palaemonidae

The representatives of Palaemonidae primarily occur in tropical and subtropical latitudes in shallow-water benthic marine or freshwater habitats. They have the highest diversity in the Indo-West Pacific region (IWP). It is a very diverse and ubiquitous family, comprising mostly species living symbiotically with other invertebrates (**Chapter 1**). The symbiotic relations of palaemonid shrimps with their host are described in detail in the section 4). Together with a limited number of free-living representatives, they also include well-known fish cleaners remarkable due to their specific behaviour (**Chapter 2**).

At present, Palaemonidae is the most speciose family of caridean shrimps with around 1,000 described species, and a series of new species are described each year. Based on molecular methods, it appears that many taxa, e.g. sponge endosymbionts, contain cryptic and pseudocryptic species. The main series of new species described in the presented thesis consists of symbiotic Pontoniinae (**Chapters 4, 7–9)**. Two new alcyonacean-associated species, *Hamodactylus paraqabai* Horká, Fransen & Ďuriš, 2016 from Papua New Guinea and the Great Barrier Reef, and *H. pseudaqabai* Horká, Fransen & Ďuriš, 2016 from Indonesia and Malaysia, were described and illustrated based on morphological and molecular data (**Chapter 4**). Three new shrimps of *Periclimenaeus* Borradaile, 1915 from the South China Sea, the Red Sea, and the Caribbean Sea, are reported in the **Chapters 7-9**; from the latter, two newly described members are obligatory endosymbionts of marine sponges, for the last species, *P. nufu* Ďuriš, Horká & Hoc, 2009 the host is unknown.

Palaemonidae has traditionally been subdivided into Palaemoninae and Pontoniinae. According to morphological end ecological characters, the palaemonine species are essentially free-living, freshwater and temperate coastal, usually larger and more slender forms, considered micro-browsers. The most speciose and best known is *Macrobrachium* Spence Bate, 1868, comprising approximately 250 species distributed worldwide in subtropical and tropical waters, commonly in freshwater rivers (e.g., Bruce 1995; De Grave and Fransen 2011; Pereira et al. 2002). One of the largest palaemonid species, *M. rosenbergii* (De Man, 1879), is particularly important in Asian aquaculture (Pereira et al. 2002; Bauer 2004).

In contrast, pontoniine shrimps are generally small-bodied, with a cryptic lifestyle (e.g., Fig. 1E, I, M in **Chapter 1**; Fig. 10A, C in **Chapter 4**), comprising the majority of symbiotic and a few free-living taxa. They are pantropically distributed in shallow and deeper marine waters, being just poorly

represented in the temperate zones and estuarine and brackish habitats (e.g., Bruce 1976a, 1995; Chace and Bruce 1993; De Grave et al. 2015).

The most prominent and well representative of pontoniine shrimps is the *Periclimenes* Costa, 1844, covering around 150 species (De Grave and Fransen 2011). Polyphyletic composition of the *Periclimenes* (e.g., Bruce 1995; Kou et al. 2013a) has led to serial cleavage of new genera. At present, based on molecular phylogenetic analyses, we clearly demonstrated that the polyphyly or paraphyly still remains even within some of those new genera, e.g., *Ancylomenes* Okuno & Bruce, 2010, *Cuapetes* Clark, 1919, or *Zenopontonia* Bruce, 1975 (**Chapters 1, 2**).

1.2 Alpheidae

After Palaemonidae, Alpheidae is the second largest family within Caridea, with around 700 described species in 47 genera (Anker et al. 2006; De Grave and Fransen 2011; WoRMS Editorial Board 2016). Alpheid shrimps represent an abundant and diverse family distributed mainly in tropical and subtropical shallow-water marine habitats. The majority of described species belong to the *Alpheus* Fabricius, 1798, comprising over 300 species (e.g., De Grave and Fransen 2011). Only a single species of this genus, *A. cyanoteles* Yeo & Ng, 1996, is truly freshwater inhabitant, while members of the *Potamalpheops* Powell, 1979 occur in either brackish or fresh waters (Bauer 2004; De Grave et al. 2008). Among alpheid genera, numerous cryptic and pseudocryptic species were discovered and confirmed in recent phylogenetic studies and systematic revisions (e.g., Knowlton and Keller 1985; Anker et al. 2007, 2009; Hultgren et al. 2014; **Chapter 5**).

Alpheid shrimps may generally be recognized by the presence of short unarmed rostrum, well-developed pair of chelae on the first pereiopods, and in most species by eyes covered dorsally by anterior projection of the carapace. The common names for these shrimps include “snapping” or “pistol” shrimps due to a large and powerful snapping chela producing a loud sound (Bruce 1985; Anker et al. 2006). The snapping sound is produced by an extraordinarily rapid closure of this large chela with the release of cavitation bubble. At the moment of bubble collapse, local energy release that leads to an extreme increase of temperature and pressure change that can stun or kill a small fish. This mechanism is used not only for hunting but it is also important in intraspecific communication (Lohse et al. 2001; Versluis et al. 2000). From the view of evolution, the completely or partially covered eyes apparently represent a protection against “shots” of snapping claw because snaps close to the head could damage them (Anker et al. 2006).

Many snapping shrimps are free-living, inhabiting dead corals, loose rubble, or sediments but large number of species are frequently found in symbioses with marine invertebrate hosts such as sponges (e.g., Duffy 1992, 1996; Hultgren et al. 2010; **Chapter 3**), cnidarians (Knowlton and Keller 1985; Hurt et al. 2013), annelids (Anker et al. 2007, 2015), echinoderms (Bruce 1976a; Criales 1984; Anker and Marin 2007) and other crustaceans, for instance stomatopods (Hayashi 2002; Ďuriš and Anker 2014), hermit crabs (Marin 2010), or upogebiid mud shrimps (Anker et al. 2001). During our survey of symbiotic shrimps in the Red Sea, three alpheid specimens of *Salmoneus* Holthuis, 1955 were collected from sandy bottom under the corals of *Acropora* Oken, 1815. These shrimps were morphologically and molecularly confirmed as a new species *S. chadwickae* Ďuriš & Horká, 2016 (**Chapter 5**). Although the true host of this new species remains unknown, most of its congeners live as symbionts in burrows inhabited by mantis shrimps or mud shrimps.

Interesting and well-known is the association of burrowing alpheid shrimps (*Alpheus* spp.) with fishes of the Gobiidae where alpheids play role of the hosts, while the fishes are symbionts. This relation is regarded mutualistic, providing benefit to both partners. The fish and usually a pair of shrimps live usually on the soft bottom habitats characterized by high predation pressure and by general lack of available shelters. The gobiid fish benefits from burrowing shrimps by obtaining a safe

shelter for itself and its eggs, while the almost blind shrimp benefits from an increased safety thanks to perfect visual system of the fish and continuous tactile contact with fish by long antennal flagella of the shrimps (Karplus et al. 1981; Karplus 1987; Bauer 2004). Overall review of partnership between gobiid fishes and alpheids is provided by Karplus and Thomson (2011).

Eusociality, the unique social organisation, was discovered by Duffy (1996) in the sponge-dwelling shrimp *Synalpheus regalis* Duffy, 1996 in the tropical western Atlantic (Fig. 1). Before, eusociality has been known only in terrestrial animals: insects (e.g., ants, honeybees, wasps, termites), and African mammals, the mole-rats (Duffy and Macdonald 1999).

Figure 1. Eusocial shrimp *Synalpheus* cf. *regalis* inside sponge *Spheciospongia vesparium* (Lamarck, 1815), Caribbean Sea. Photo by Z. Ďuriš.

The shrimp eusociality is characterized by a cooperative colony that may contain over 300 individuals from which most members sacrifice own reproduction for one reproductive female (the queen). Eusocial *Synalpheus* species don't produce planktonic larvae, the embryos hatch as crawling juveniles which mainly stay in the host sponge. The eusocial colony organization originated three times independently within *Synalpheus* species of the *S. gambarelloides* group. The evolution of eusociality is conditioned by limited availability of hosts or high enemy pressure, when cooperative social groups have a competitive advantage (Duffy et al. 2000; Bauer 2004). A general model highlighting key factors affecting the social behaviour of symbiotic crustaceans was proposed by Thiel and Baeza (2001) (Fig. 2). Apparently, the ability to defend host and mobility of shrimps has strong effects on the social behaviour. In addition, reproductive mode of symbiotic crustaceans is also very important.

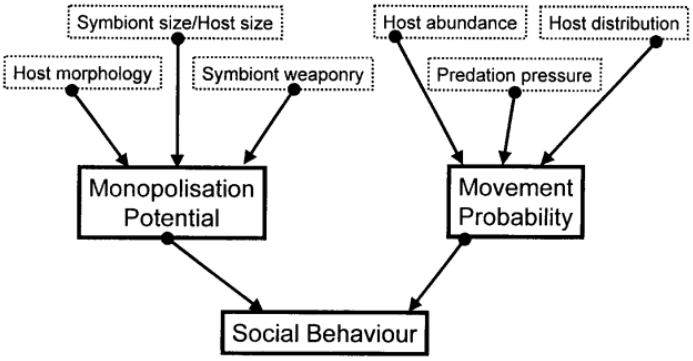


Figure 2. Model summarizing the factors that shape the social behaviour of symbiotic crustaceans (adopted from Thiel and Baeza 2001). It shows that the ability to defend host (monopolizing potential) and mobility (probability of intraspecific encounters) have strong effects on the social behaviour.

1.3 Pandalidae

Pandalidae is a family of predominantly cold marine water species (comprising 23 genera and cca 200 species) occurring on both northern and southern hemispheres, with the greatest diversity in subpolar to temperate Atlantic and Pacific waters (Bauer 2004; De Grave and Fransen 2011). In the tropical regions, the pandalid shrimps are represented by deep-sea species usually living on soft substrates; some species were caught at depths exceeding 3,000 meters (Chace 1985; Bruce 1983).

From the commercial point of view, Pandalidae is the most important family of caridean shrimps (Holthuis 1980). Particularly, some species of *Pandalus* Leach, 1814, *Pandalopsis* Spence Bate, 1888, and *Heterocarpus* A. Milne-Edwards, 1881 are widely used in fisheries (Komai and Eletskaya 2008; Bauer 2004). Typical pandalids are free-living, medium to large sized, with long slender legs and rostrum (Bruce 1983). Their first pereiopods are slender, with simple or microscopic chelae, the second pereiopods with small chelae are used in food searching, feeding, and grooming. Pandalid shrimps are mainly characterised by the carpus of the second pereiopod subdivided into multiple subsegments (Chace 1985; Bauer 2004).

Symbiotic relationships are very rare in Pandalidae, and to present, only three obligate symbionts have been reported: *Anachlorocurtis commensalis* Hayashi, 1975, *A. occidentalis* Horká, De Grave & Ďuriš, 2014 (**Chapter 6**), and *Miropandalus hardingi* Bruce, 1983. All of them were found associated with antipatharian black corals (Anthozoa, Antipatharia) (Hayashi 1975; Bruce 1983, 1991). *Anachlorocurtis commensalis* is known from Japan and Taiwan, *A. occidentalis* is currently only known from its type locality, Gulf of Aqaba, in the north-eastern Red Sea (**Chapter 6**). *Miropandalus hardingi* was reported from Marshall Islands (type locality), Japan and Taiwan (Bruce 1983, 1991; **Chapter 6**). The external morphology of both *Anachlorocurtis* Hayashi, 1975 and *Miropandalus* Bruce, 1983 is unique, with their body being modified to living with their hosts (Fig. 3A). They are small, slender, and laterally compressed animals with a cryptic colour and shape (**Chapter 6**), short (*Anachlorocurtis*), or fully reduced (*Miropandalus*) rostra, specialised mouth-parts, and a low number of comparatively large eggs (Hayashi 1975; Bruce 1983, 1991).

The associations with invertebrate hosts in other pandalid shrimps, e.g., *Chlorotocella gracilis* Balss, 1914 or *Chlorocurtis jactans* (Nobili, 1904) (Z. Ďuriš and author, pers. obs.), are sparse and feeble. Facultative associations are reported for some species of genus *Pandalus*, e.g., for *Pandalus tridens* Rathbun, 1902 with the sea anemone *Cribrinopsis fernaldi* Siebert & Spaulding, 1976 in Alaskan waters (Stevens and Anderson 2000).

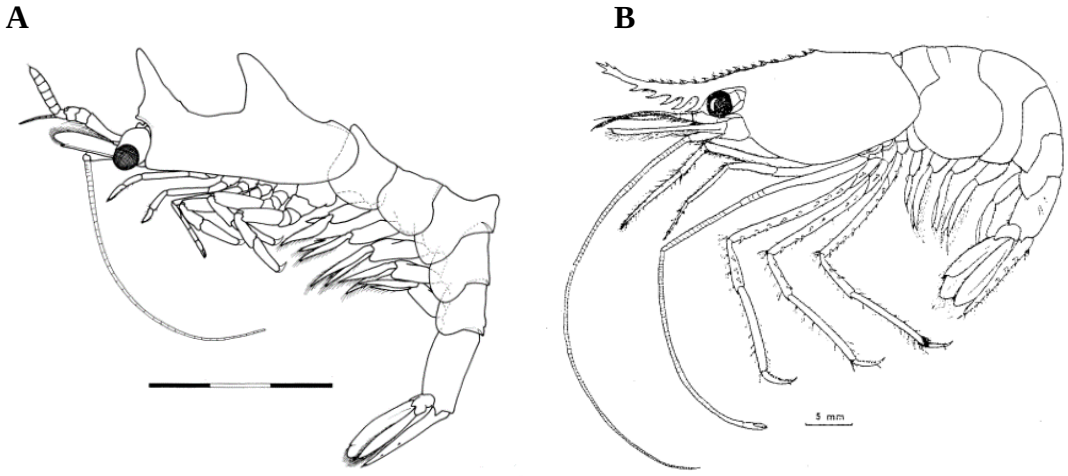


Figure 3. Symbiotic and free-living pandalid shrimps. A, symbiotic *Miropandalus hardingi* associated with black corals (Antipatharia); B, free-living *Pandalus gracilis* Stimpson, 1860. Figures adopted from Bruce (1983) and Hayashi (1988), respectively.

1.4 Thoridae

The species of the newly established family Thoridae were previously placed in Hippolytidae which contains over 340 described species in 42 genera, was the fourth largest family within Caridea (De Grave and Fransen 2011; WoRMS Editorial Board 2016). De Grave et al. (2014) rejected the monophyletic Hippolytidae and recognized five families based on molecular study: Hippolytidae, Lysmatidae, Thoridae, Bythocarididae and Merguiidae within the superfamily Hippolytoidea. The general morphological features of Hippolytoidea shrimps are: (1) the first pair of pereiopods is distinctly chelate and moderately robust; (2) the second pair is elongated and slender, frequently with multi-segmented carpus; (3) the rostrum is usually dentate, not covering the eyes (Bruce 1985; Holthuis 1993). They occur worldwide, with largest diversity in colder regions, particularly in the north Pacific (Bauer 2004). Only Thoridae and Lysmatidae comprise some genera with symbiotic relationships to tropical cnidarians, predominantly the giant sea anemones.

The most common, conspicuous, and also best known general symbiont within Thoridae is *Thor amboinensis* (de Man, 1888) reported from all tropical oceans, and also from the Canary and Madeira Islands (Wirtz 1997; Bauer 2004). This species was reported from several species of sea anemones, and cerianthid tube dwelling anemones (e.g., Guo et al. 1996; Chadwick et al. 2008), crinoids (Criales 1984), or mantis shrimps (Debelius 1999). While the symbiotic associations are generally common in tropical waters, the associations of some thorid species are unique due to their geographic distribution also in the northern Pacific (Bering Sea), the northern Atlantic (Labrador Sea), as well as in the Southern Ocean (e.g., Stevens and Anderson 2000). In the Northern Hemisphere, the thorid shrimps of genera *Lebbeus* White, 1847, *Eualus* Thallwitz, 1892, and *Spirontocaris* Spence Bate, 1888 were reported as associated with the sea anemones *Bolocera* Gosse, 1860, *Cribrinopsis* Carlgren, 1921, or *Metridium* de Blainville, 1824 (e.g., Stevens and Anderson 2000; Schiaparelli et al. 2015). These associations were evaluated by Stevens and Anderson (2000) as facultative, and the shrimps as commensal or mutualist symbionts.

1.5 Lysmatidae

The newly established family Lysmatidae includes five genera: *Ligur* Sarato, 1885, *Lysmata* Risso, 1816, *Mimocaris* Nobili, 1903, *Lysmatella* Borradaile, 1915, and *Exhippolysmata* Stebbing,

1915 (De Grave et al. 2014). This family is less significant from the host association point of view. Up to the present time, only three species of *Lysmata* from the eastern Atlantic and the Caribbean were reported in association with sea anemones: *Lysmata ankeri* Rhyne & Lin, 2006, *L. grabhami* (Gordon, 1935), and *L. seticaudata* (Risso, 1816). The observations indicate that these shrimps are facultative anemone symbionts, and the host is preferred mainly by adult and subadult individuals, while juveniles occur on corals (e.g., Criales 1979, 1984; Wirtz 1997; Wirtz et al. 2009). The species of genus *Lysmata* are much more known as the cleaner shrimps. Five species were reported as cleaners of fishes from different families, e.g., Acanthuridae, Labridae, Muraenidae, Pomacentridae or Serranidae, and even of the spiny lobster *Panulirus interruptus* (Randall, 1840) (Limbaugh et al. 1961; Wicksten 2009).

The cleaning symbiosis, despite focused mainly to another family, is object of the section 4.6 and the **Chapter 2** of this thesis, where it is described and discussed in more detail.

2. Systematics of Palaemonidae

A significant portion of crustacean diversity on coral reefs is formed by caridean shrimps with almost 400 genera and more than 3,400 species described (De Grave and Fransen 2011). It is the second most diverse group in decapod crustaceans (order Decapoda). The carideans belong to the suborder Pleocyemata erected by Burkenroad (1963), and are distributed widely around the world in fresh and marine habitats. The key characters of the infraorder Caridea are: fertilised eggs are incubated by females on pleopods under their abdomen until zoea larvae are ready to hatch; the gills are lamellar (Abele and Felgenhauer 1982; Bauer 2004). At present, 14 superfamilies with 39 families are recognised in Caridea, dominated by Palaemonidae, and followed by Alpheidae (De Grave and Fransen 2011; De Grave et al. 2014, 2015; WoRMS Editorial Board 2016).

Palaemonidae had traditionally included: Euryrhynchinae, Typhlocaridinae, Pontoniinae and Palaemoninae (e.g., Holthuis 1951). Chace (1992) and Holthuis (1993) performed the revision of caridean families and subfamilies, and explained the separation of two subfamilies, Palaemoninae and Pontoniinae, on the basis of the number of telson spines (Chace 1992) and presence or absence of the pleurobranch above the third maxilliped (Holthuis 1993). The subfamily Palaemoninae is defined by two pairs of spines at the posterior end of the telson with feathered setae between them, and presence of a pleurobranchia on the third maxilliped. The presence of three pairs of spines at the posterior end of the telson and the absence of pleurobranchia on the third maxilliped defined the Pontoniinae (Holthuis 1993; Pereira 1997).

The actual superfamily Palaemonoidea contains five families: Anchistioididae, Desmocarididae, Euryrhynchidae, Palaemonidae, and Typhlocarididae (De Grave et al. 2015). For a long time, the Hymenoceridae and Gnathophylidae were included into Palaemonoidea as taxa separately positioned out of the above families (De Grave et al. 2009), although already Bruce (1986, 1988) suggested, that these two families would be included into Palaemonidae based on larval morphology. The conspicuous morphological resemblance among pontoniine and gnathopyllid larvae was later confirmed also by Yang and Ko (2004).

Recently, based on molecular methods, it became obvious that Palaemonidae is polyphyletic (e.g., Bracken et al. 2009), with Gnathophyllidae and Hymenoceridae situated within Pontoniinae (Mitsuhashi et al. 2007; Kou et al. 2013b; Gan et al. 2015a,b; De Grave et al. 2015; **Chapter 1**). Molecular study (**Chapter 1**) of symbiotic palaemonid shrimps, including also hymenoceroid and gnathophyllid representatives, likewise confirms the polyphyletic status of several genera within Palaemonidae.

3. General morphology of palaemonid shrimps

The body of caridean shrimp is divided into three main regions: head (cephalon), thorax, and abdomen (pleon). The major morphological features of palaemonid shrimps are demonstrated in Figure 4. The first two regions are rigidly fused to a single unit, the cephalothorax, which is dorsally and laterally covered by the cephalo-thoracic shield, the carapace, which provides protection for the vulnerable internal organs; its lateral folds form the gill chambers. In some species, the carapace bears a prominent anterior projection called the rostrum. The carapace can be equipped with spines, tubercles, keels, ridges, or grooves that may be taxonomically important. On the shrimp body there are nineteen pairs of appendages, each attached to one of the body segments (somites), and they are grouped as follows: head – 5 pairs, thorax – 8 pairs, abdomen (pleon) – 6 pairs (e.g., Schmitt 1921; Moore 1969).

The first pair of cephalic appendages is represented by the antennules (or antennae I) which consist of three segment peduncle. In the proximal segment, there is an equilibrium organ (statocyst) that contains mechanoreceptor setae responsive to changes in spatial orientation (Boxshall and Jaume 2013). The statocysts of caridean shrimps are protected by the antennular scale (stylocerite), which protects the opening of the statocyst (Moore 1969). The antennules bear two flagella (in most Palaemonidae) of variable length, the inner and outer, the latter divided into two branches. The outer flagellum bears the aesthetascs used for chemoreception. The second pair of cephalic appendages are antennae (or antennae II). Their basal two-segmented protopodite bears outer antennal scale or squama (scaphocerite), and a long flagellum with tactile and chemical receptors (Moore 1969; Bauer 2004).

The eyes are not considered true appendages (Schmitt 1921). The large, stalked compound eyes are fully developed in free-living species, while they are reduced in symbiotic representatives in varying degrees (Dobson et al. 2014).

The following three pairs of cephalic appendages belong to mouthparts, and include the mandibles, and the first and second maxillae. The mandibles with a strongly calcified body are used for food intake and handling. They consist from the incisor and molar process. The first one is used for biting and cutting, and the second one for crushing and grinding food particles. In many caridean shrimps, a small (no more than three-segmented) palp is present on mandibles, but it can be reduced or absent in some cases (Moore 1969; Bauer 2004). Some authors consider the presence of palp in shrimp as phylogenetically primitive character (e.g., Thompson 1967). The presence of palp in pontoniine shrimps is mentioned, e.g., for the genera *Eupontonia* Bruce, 1971, *Exoclimenella* Bruce, 1995, *Palaemonella* Dana 1852, or *Vir* Holthuis, 1952 (Bruce 1995; Ďuriš and Bruce 1995).

The two pairs of maxillae, also termed as the maxillules and the maxillae, are weakly calcified. Their function is performed by the exopod of the maxilla (scaphodnathite) which is extended anteriorly and posteriorly and which pumps the respiratory stream of water out of the exhalant canal of the branchial cavity (Moore 1969). A detailed description of shrimp mouthparts is usually an integral part of descriptions of new species (**Chapters 4-9**).

The next eight segments of the body are thoracic, bearing the first, second and third maxillipeds used for food manipulation, and five pairs of walking legs (pereiopods 1–5). The first two pairs of caridean shrimp pereiopods are equipped with claws (chelae) and termed chelipeds. The chela consists from the fixed finger (propodus) and the movable finger (dactylus). The first pair of pereiopods is slender and symmetrical, with only small chelae, whereas the second pair of pereiopods is much more strongly developed with large chelae, which may be similar and equal on each side of the body, or dissimilar and unequal (Bruce 1985). The chelae of the second pereiopods are the main means of defence. Some members of Pontoniinae can produce snaps and pops with chelipeds, similarly to unrelated alpheid shrimps (see Bruce 1976a; Moore 1969; Bauer 2004). Snapping with sound production evolved several times in pontoniines. Up to the present, it was reported in genera

Coralliocaris Stimpson, 1860, *Harpiliopsis* Borradaile, 1917, *Jocaste* Holthuis, 1952, *Onycocaris* Nobili, 1904, *Paraclimenaeus* Bruce, 1988, *Periclimenella* Bruce, 1995, *Periclimenaeus*, and *Thaumastocaris* Kemp, 1922. The principle of sound production varies depending on the shape of chelipeds. For instance, species of *Periclimenaeus* produce sounds by one modified claw using the molar process on the dactylus, similarly as alpheids, but on the second pereiopod. Some members of *Coralliocaris* have developed this mechanism on both claws, and the sound can be produced simultaneously; *C. graminea* (Dana, 1852) is considered to be one of the best producers of snapping noises on coral reefs (Bruce 1976a,b 1995).

The posterior three pairs of pereiopods in palaemonid shrimps are simple and they are also called ambulatory legs (Schmitt 1921). Particularly, the dactyls of symbiotic species show a great variety of modifications including the formation of various teeth and hooks. These adaptations are well developed mainly in the sponge, tunicate or mollusc endosymbionts (Bruce 1976b).

The abdomen is composed of six true somites and one flattened segment, the telson, which never bears appendages and is not considered true somite (Schmitt 1921). The telson originates as a protrusion of the previous abdominal segment and its primary function is to bear the anus on its lower side (Moore 1969; Bauer 2004). The first five pairs of abdominal appendages are the pleopods, used for paddling in forward swimming. They are biramous with a short coxa and longer basis. Female pleopods are all identical and modified for incubation of eggs and embryos, while the first two pleopods in males are modified as gonopods and they have reproductive function. The endopod of the second male gonopods bears the appendix masculina, alongside the appendix interna. Experimental works have shown that appendix masculina is used in copulation and spermatophore transfer (Moore 1969; Bauer 2004).

The last pair of abdominal appendages is termed uropods. They constitute together with the telson the so-called tail-fan, important for forward and backward swimming and escape from predators. In caridean shrimps, it is typical that the pleura of the second segment overlap those of the first and third, and the abdomen is strongly curved downward in normal position. This facilitates the protection of the eggs during its incubation. In stenopodidean and dendrobranchiate shrimps, the first pleura overlaps the second, the second the third, and so on down the abdomen (Moore 1969; Christoffersen 1988; Bauer 2004).

Descriptions of new species of caridean shrimps from Palaemonidae (sensu Pontoniinae), Alpheidae and Pandalidae with the use of represented morphological features are presented in the **Chapters 4-9**.

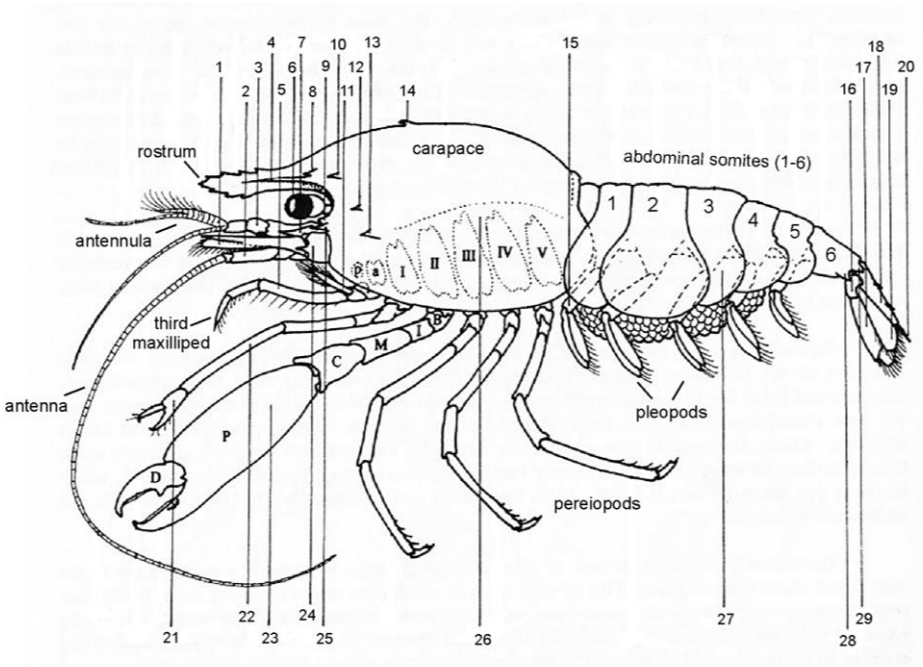


Figure 4. The major morphological features of palaemonid shrimps, lateral view (after Bruce 1995; modified). **1**, scaphocerite; **2**, carpocerite; **3**, intermediate segment of antennular peduncle; **4**, lateral rostral carina; **5**, antepenultimate segment of third maxilliped; **6**, cornea; **7**, stylocerite; **8**, supraocular spine; **9**, inferior orbital angle; **10**, supraorbital spine; **11**, exopod of third maxilliped; **12**, postorbital spine; **13**, hepatic spine; **14**, epigastric spine; **15**, basipodite of first pleopod; **16**, protopodite of uropod; **17**, exopod of uropod; **18**, telson; **19**, endopod of uropod; **20**, posterior telson spines; **21**, chela of first pereiopod; **22**, carpus of first pereiopod; **23**, palm of chela of second pereiopod; **24**, basicerite; **25**, antennual spine; **26**, branchiostegite; **27**, pleuron of third abdominal segment; **28**, posteroventral angel of 6th abdominal segment; **29**, posterolateral angle of 6th abdominal segment. Branchiae; **P**, podobranch of second maxilliped; **A**, arthrobranch of third maxilliped; **I-V**, pleurobranchs of 4th to 8th thoracic segments. Segments of pereiopods; **D**, dactyl; **P**, propod; **C**, carpus; **M**, merus; **I**, ischium; **B**, basis.

4. Symbioses in palaemonid shrimps

Symbiotic palaemonid shrimps (Pontoniinae *sensu* De Grave and Fransen 2011) usually occur in association with a variety of different hosts organisms – from sponges, corals and sea anemones to molluscs, echinoderms and ascidians (e.g., Bruce 1972; 1975, 1982; Marin 2007; **Chapter 1**), less often with other decapod crustaceans (Bruce and Okuno 2006). De Grave (2001) and Li et al. (2003) estimate about 60–80 % of pontoniines to be symbiotic; according to Dobson et al. (2014) those values are still underestimated.

The symbiotic mode of life caused various morphological adaptations in symbiotic palaemonid (= pontoniine) shrimps during their evolution, including changes in general body size and shape, reduction or elimination of spines and processes, modifications of pereiopods, or specific formation of eyes and mouthparts (Bruce 1995). In addition to morphological adaptations, many shrimps show adaptive colour pattern that is related to the colour of their host. Species living on the host surface in the exposed conditions are often cryptic coloured (**Chapter 6**), others prefer the different strategy of being more or less transparent or having disruptive coloration. Shrimps living safely inside their hosts may have bright and conspicuous colours (Bruce 1976a,b). Reproductive or behavioural adaptations of symbiotic palaemonids are also often remarkable (e.g., Bruce 1976b; Dobson et al. 2014).

The following sections describe the known general host phyla of pontoniines, i.e., Porifera, Cnidaria, Mollusca, Tunicata and Echinodermata. Furthermore, I discuss the specific type of mutualistic relations, the cleaning symbiosis.

4.1 Sponge-dwelling shrimps

Marine sponges (phylum Porifera), particularly class Demospongiae, are hosts for many pontoniine genera. Their morphological architecture with one or more large oscula, and the body interwoven by a vast network of canals of varying diameter, provide excellent shelter for abundance of small-sized symbiotic shrimps. The sponge-inhabiting pontoniines are represented by more than 20 genera; the following of them are obligatory associated: *Apopontonia* Bruce, 1976, *Climeniperaeus* Bruce, 1995, *Epipontonia* Bruce, 1977, *Holthuisaeus* Anker & De Grave, 2010, *Nippontonia* Bruce & Bauer, 1997, *Onycocaridella* Bruce, 1981, *Onycocaridites* Bruce, 1987, *Onycocaris*, *Orthopontonia* Bruce, 1982, *Paraclimenaeus*, *Periclimenoides* Bruce, 1990, *Plesiomenaeus* Bruce, 2009, *Poripontonia* Fransen, 2003, *Thaumastocaris*, *Typtonomenaeus* Marin & Chan, 2013, and *Typtonychus* Bruce, 1996.

In other genera, such as *Anisomenaeus* Bruce, 2010, *Exopontonia* Bruce, 1988, *Hamiger* Borradaile, 1916, *Pseudoclimenes* Bruce, 2008 or *Typtonoides* Bruce, 2010, the association with sponges is assumed (Bruce 1995, 2008, 2010). The majority of these genera are monotypic (see Marin and Chan 2013) with unique morphological features.

The species-rich genus *Periclimenaeus*, consisting actually of around 70 species, is roughly equally divided among ascidian- as well as sponge-associated endosymbionts (Fransen 2003, 2006; **Chapters 3, 7, 8**). The possible paraphyly of this genus was indicated based on phylogenetic studies (Gan et al. 2015; **Chapter 1**).

Until recently, the genus *Typton* Costa, 1844 was known only as sponge-associated (e.g., Bruce 1976b, 1995; **Chapter 3**; Marin 2015) but a species living with holothurians was discovered as well (Ayón-Parente et al. 2015).

Above-mentioned sponge-dwelling genera are endosymbionts, only three species of *Periclimenes* are considered as sponge facultative ectosymbionts: *P. colesi* De Grave & Anker, 2009, *P. incertus* Borradaile, 1915, or the dee-sea *P. forcipulatus* Bruce, 1991 (Bruce 1976b; Li and Bruce 2006).

Endosymbiotic sponge-dwelling shrimps are well morphologically adapted to small tubular spaces in their host (Fig. 5). These shrimps are generally small, with elongate subcylindrical body lacking the hepatic spine on the sides of the carapace (*Periclimenaeus*, *Thaumastocaris*), and often with a reduced rostrum (*Onycocaridella*) and scaphocerites (*Onycocaris*, *Typton*).

The sponge-inhabiting pontoniine shrimps live in heterosexual pairs, and especially males possess large chelipeds for fights with conspecifics. In addition to that, the major claw of the most speciose sponge-endosymbiotic genus *Periclimenaeus* (as well as *Holthuisaeus*) is armed by a sound-producing apparatus similar to that of the snapping shrimps (Alpheidae, section 1.2). Sound production is known also in *Thaumastocaris* or *Onycocaris* spp. but without special mechanism evolved (Bruce 1976b, 1995; Marin 2015).

Shrimps with symbiotic associations with sponges are often referred as spongobionts, commensals, inhabitants, or associates, without specifying the actual nature of the symbiosis. Endosymbiotic life in sponges is specific regarding available food sources. Many, if not most, sponge-inhabiting shrimp species had to develop abilities to feed on the sponge tissues, i.e., their ‘home’, at least to a limited extent (**Chapter 3**). We demonstrated, based on the detailed examination of morphology and the stomach contents that shrimps of the genera *Typton*, *Onycocaris*, *Periclimenaeus*, and *Thaumastocaris* are parasites which consume the sponge tissue. However, it is also possible that those shrimps provide a service to the host sponge by preventing a penetration by potentially more damaging associated animals.

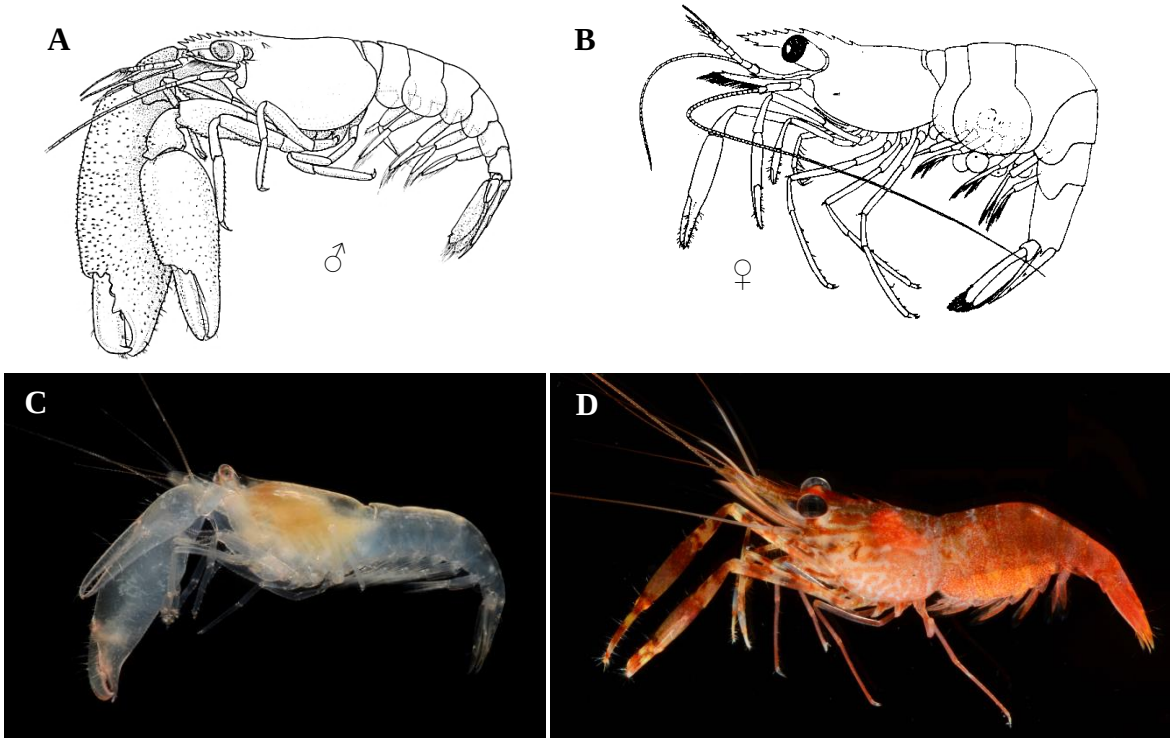


Figure 5. **Diversity of body form and colouration of sponge-associated shrimps.** A, *Periclimenaeus echinimanus* Ďuriš, Horká & Al-Horani, 2011; B, *Periclimenes incertus* Borradaile, 1915; C, *Holthuisaeus bermudensis* (Armstrong, 1940); D, *Brachycarpus biunguiculatus* (Lucas, 1846). A, C - endosymbionts, B, D - ectosymbionts. Figures adopted from Ďuriš et al. (2011) and Kemp (1922); photos by Z. Ďuriš.

4.2 Cnidarian-associated shrimps

Pontoniine shrimps associated with cnidarians, predominantly with hard and soft corals and sea anemones, are abundant on most coral reefs in the IWP and tropical western Atlantic, and represent a major diversity of the symbiotic caridean shrimps (Bruce 1976a, 1977). According to the ancestral state analysis presented in this thesis (**Chapter 1**), the cnidarian ectosymbionts were generally the primary ancestors, from which all ectosymbioses with other hosts, as well as endosymbioses with another ones, subsequently evolved.

One of the most distinctive, and evolutionary most progressive cnidarian-associated genus is *Ancylomenes* (Fig. 7). At present, around 20 species are known. These were observed predominantly in associations with sea anemones, but some live also on scleractinian corals, ceriantharians and benthic jellyfish (e.g., Bruce 2008, 2013; Okuno and Bruce 2010). *Ancylomenes* species often occur with hosts in large social groups and can swim freely around their hosts (Chadwick et al. 2008). In contrast, some other anemone-associated shrimps such as *Periclimenes brevicarpalis* (Schenkel, 1902) or *P. ornatus* Bruce, 1969, live exclusively as obligatory associates with their host in heterosexual pairs and leave their anemone only if they are strongly disturbed (Chadwick et al. 2008). Cnidarian-associated pontoniine shrimps are represented exclusively by ectosymbionts, with a single exception, *Paratypton siebenrocki* Balss, 1914 (Fig. 6A), living inside cysts or galls of corals of *Acropora* (Bruce 1969, 1995).

As in other symbiotic shrimps, the coevolution with hosts leads to different adaptations. The morphological adaptations are conspicuous especially in some coral-associated genera. For example, genera *Coralliocaris* or *Harpiliopsis* are well adapted to life among the branches of coral colonies (Bruce 1977). *Ischnopontonia* Bruce, 1966 with extremely laterally compressed body (Fig. 6C) and *Platycaris* with strongly depressed body (Fig. 6B) exclusively live as symbionts in specific narrow

spaces among corallites of the oculinid coral *Galaxea fascicularis* (Linnaeus, 1767); both shrimps are representatives of specialized monospecific genera (Bruce 1976a,b).

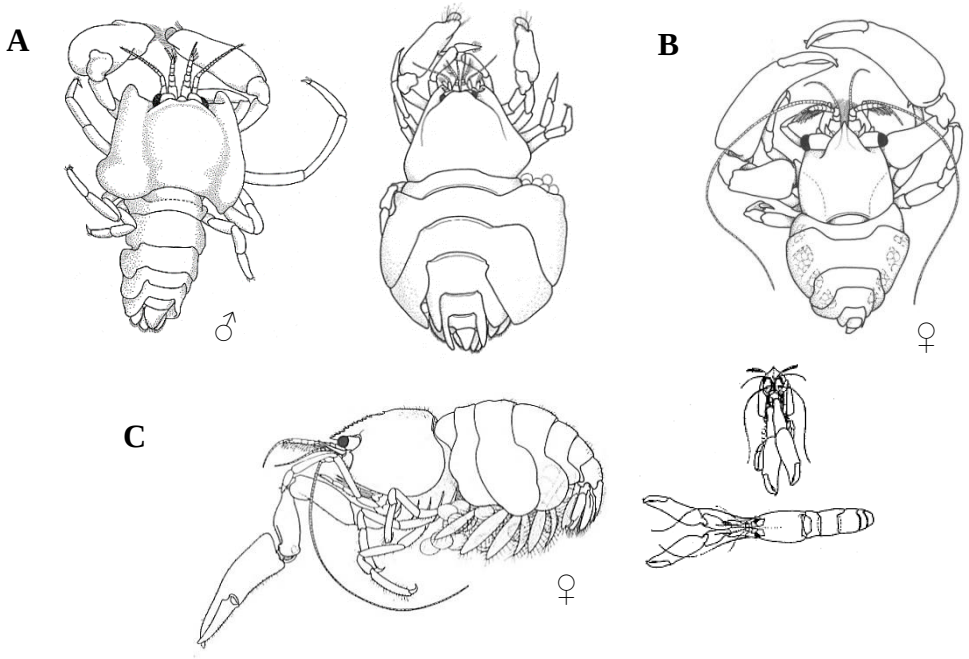


Figure 6. Obligatory coral-associated species with specific morphological adaptations. A, *Paratypton siebenrocki* living encased in coral cyst; B, *Platycaris latirostris* with dorsoventrally compressed body; C, *Ischnopontonia lophos* (Barnard, 1962) with strongly laterally compressed body. Figures adopted from Bruce (1969, 1995).

Figure 7. Colour patterns on transparent body of symbiotic *Ancylomenes* species from the Red Sea. A, anemone-associated *Ancylomenes longicarpus* (Bruce & Svoboda, 1983); B, *A. aqabai* (Bruce, 2008) associated with up-side down jellyfish *Cassiopea andromeda* (Forskål, 1775); photos by author.

4.3 Mollusc-associated shrimps

Up to the present, 10 genera (with >40 spp.) of pontoniines are known as endosymbionts of marine molluscs, namely: *Anchiopontonia* Bruce, 1992, *Anchistus* Borradaile, 1898, *Bruceonia* Fransen, 2002, *Cainonia* Bruce, 2005, *Conchodytes* Peters, 1852, *Neoanchistus* Bruce, 1975, *Paranchistus* Holthuis, 1952, *Pinnotherotonia* Marin & Paulay, 2010, *Platypontonia* Bruce, 1968, and *Pontonia* Latreille, 1829. The genera *Anchiopontonia*, *Bruceonia*, *Cainonia*, and *Pinnotherotonia* are monotypic (e g. Fransen and Meij 2010; De Grave and Fransen 2011; Fransen and Reijnen 2012).

Most species of the pontoniine shrimps live symbiotically inside the mantle cavity of lamellibranch bivalves; only one species, *Pontonia chimaera* Holthuis, 1951, was reported as associated with the large gastropod *Strombus galeatus* Swainson, 1823 (Holthuis 1951; Marin and Anker 2008). The highest diversity of bivalve-associated pontoniine species (~80%) are known from the tropical Indo-West Pacific region followed by the Atlantic basin (~13%) and the tropical Eastern Pacific (~7%). Symbiotic members were recorded from the bivalve mollusc families (e.g., Pinnidae, Placunidae, Ostreidae, Spondylidae, Pectinidae, or Cardiidae) of which most species are epifaunal. Only two pontoniine shrimps, i.e., *Pinnotherotonia rumphiusi* Marin & Paulay, 2010 and *Neoanchistus cardiodytes* Bruce, 1975, have been documented inside burrowing bivalves that belong to one of the less explored mollusc hosts (Marin and Paulay 2010). The taxonomical revision of *Pontonia* (sensu lato) based on phylogenetic analysis using morphological characters was performed by Fransen (2002) who established five new genera. Since then, *Pontonia* (sensu scricto) includes mostly mollusc-associated species, with the exception of *P. panamica* Marin & Anker, 2008 living inside ascidians (Marin and Anker 2008).

The conspicuous morphological adaptations in bivalve-associated shrimps are connected with the narrow and confined space in the host mantle cavity. The bodies of some shrimps are strongly depressed or flattened with short stout appendages, such body form is particularly developed in *Conchodytes placunae* (Johnson, 1967) living in the greatly flattened bivalve *Placuna placenta* (Linnaeus, 1758) (Johnson 1967; Bruce 1976a, 1995). In contrast, the body of the other *Conchodytes* species is often greatly swollen and smooth, which is related with sufficient space for movement inside other bivalve molluscs (Fig. 8A-C). The rostrum of bivalve-associated shrimps is also usually much reduced in size, blunt and with few or very small teeth, and in some cases it is entirely toothless. Many of the spines usually found on caridean shrimps, such as hepatic, antennal or abdominal spines, are reduced or lost as well. The well-developed chelae on the second male pereiopods are the main means of defence against colonisation by conspecifics (Bruce 1972, 1976a, 1995).

Relatively little known are biology and character of relation in these mollusc endosymbionts. The feeding habit of *Anchistus custos* (Forskål, 1775) was studied by Johnson and Liang (1966) who reported that it is a commensal without harmful effect on the host. The shrimps normally cling to the edge of the host gill lamellae and scrape the mucus containing mainly diatoms and detritus by their highly modified chelae of the first pereiopods (Bruce 1972). The host mantle cavity serves not only the food source but it is also the protective shelter for shrimps (Bauer 2004). Shrimps leave their host immediately on its death (Johnson and Liang 1966).

Shrimps occupying the bivalve mantle cavities are always found in heterosexual pairs, only sometimes the juveniles may be present together with them. The sexual dimorphism is noticeable; the female is larger and shows less developed chelae than the male (Bruce 1972). Baeza and Thiel (2007) predicted that marine symbiotic crustaceans, inhabiting small hosts in tropical regions where predation risk is high, are monogamous. This presumption was studied in shrimps *Paranchistus pycnodontae* Bruce, 1978, *Pontonia margarita* Verrill, 1869 and *P. mexicana* Guérin-Méneville, 1855 (Fig. 8D) and it was confirmed that these species are found more frequently as heterosexual pairs inside the mantle cavity of bivalve host; the major chela of males did not show positive allometry that is generally reported for polygamous shrimps, and males occur with females independently whether the female carries eggs or not, and in what developmental stage eggs are (Baeza 2008; Baeza et al. 2011, 2013, 2015).

Only one species, *Zenopontonia rex* (Kemp, 1922), is known as ectosymbiont of nudibranch gastropods, but frequently it is also found associated with crinoids or holothurians (Fransen and Gould 2000).

4.4 Ascidian-associated shrimps

Another group hosting shrimp endosymbionts are representatives of the class Ascidiacea (subphylum Tunicata), commonly known as ascidians or sea-squirts. They are found worldwide, in both marine shallow and deep water. Adult animals are sessile, firmly attached to a substrate. Some ascidian species are solitary or unitary; their individuals are physically separated of each other. Other ascidian representatives are physically and functionally connected and form colonies composed from thousands of microscopic individuals. Relatively few species of shrimps are found in association with ascidians. Among pontoniine shrimps, ten genera are known to date: *Amphipontonia* Bruce, 1991, *Ascidonia* Fransen, 2002, *Colemonia* Bruce, 2005, *Dactylonia* Fransen, 2002 (Fig. 8E), *Dasella* Lebour, 1945, *Odontonia* Fransen 2002, *Periclimenaeus*, *Pontonia*, *Pseudopontonia* Bruce, 1992, and *Rostronia* Fransen, 2002 (Bruce 1976a,b; Fransen 2002, 2006).

Ascidian-associated shrimps occupy two different groups of Ascidia with distinctive morphologies and have body plans analogous to sponge- or bivalve-inhabiting shrimps (section 4.1, 4.3); their morphological adaptions are also related to limited space inside their hosts (Fig. X). The solitary ascidians of relative large, macroscopic, bag-like bodies (e.g., *Polycarpa* Heller, 1877, *Pyura* Molina, 1782, *Rhopalaea* Philippi, 1843 or *Styela* Fleming, 1822) are occupied in their branchial chamber mainly by shrimps of genera *Ascidonia*, *Dasella*, *Odontonia* or *Rostronia*. The compound, colonial ascidians (e.g., *Didemnum* Savigny, 1816, *Exostoma* Kott, 1990, *Hypodistoma* Tokioka, 1967) with network of narrow subdermal channels structurally similar to the internal canals of sponges are inhabited by species of *Periclimenaeus*, other members associated with sponges. The *Periclimenaeus* spp. are generally very small and cryptic in their ecology, thus quite a lot of them are only known from one or few specimens (Fransen 2002, 2006; **Chapters 7-9**).

The true character of relation of the shrimps to ascidian hosts remains widely unknown. The major component of shrimp food most likely represents mucus and detritus produced or collected by their ascidian host. Shrimps also can obtain food on external surface of their hosts, or in the neighbouring area.

The symbiotic crustaceans that occur in or on small (relative to symbiont body size), scarce and structurally simple hosts, are expected to live solitarily (e.g., Baeza and Thiel 2007). That is true, e.g., for the ascidian-associated shrimp *Ascidonia flavomaculata* (Heller, 1864) frequently found as a single individual in the branchial cavity of sea squirts. It was observed that males and females of *A. flavomaculata* actively swim among host individuals. Males probably search sexual partners, and females may search for larger host to obtain more resources during summer months (Baeza and Díaz-Valdés 2011).

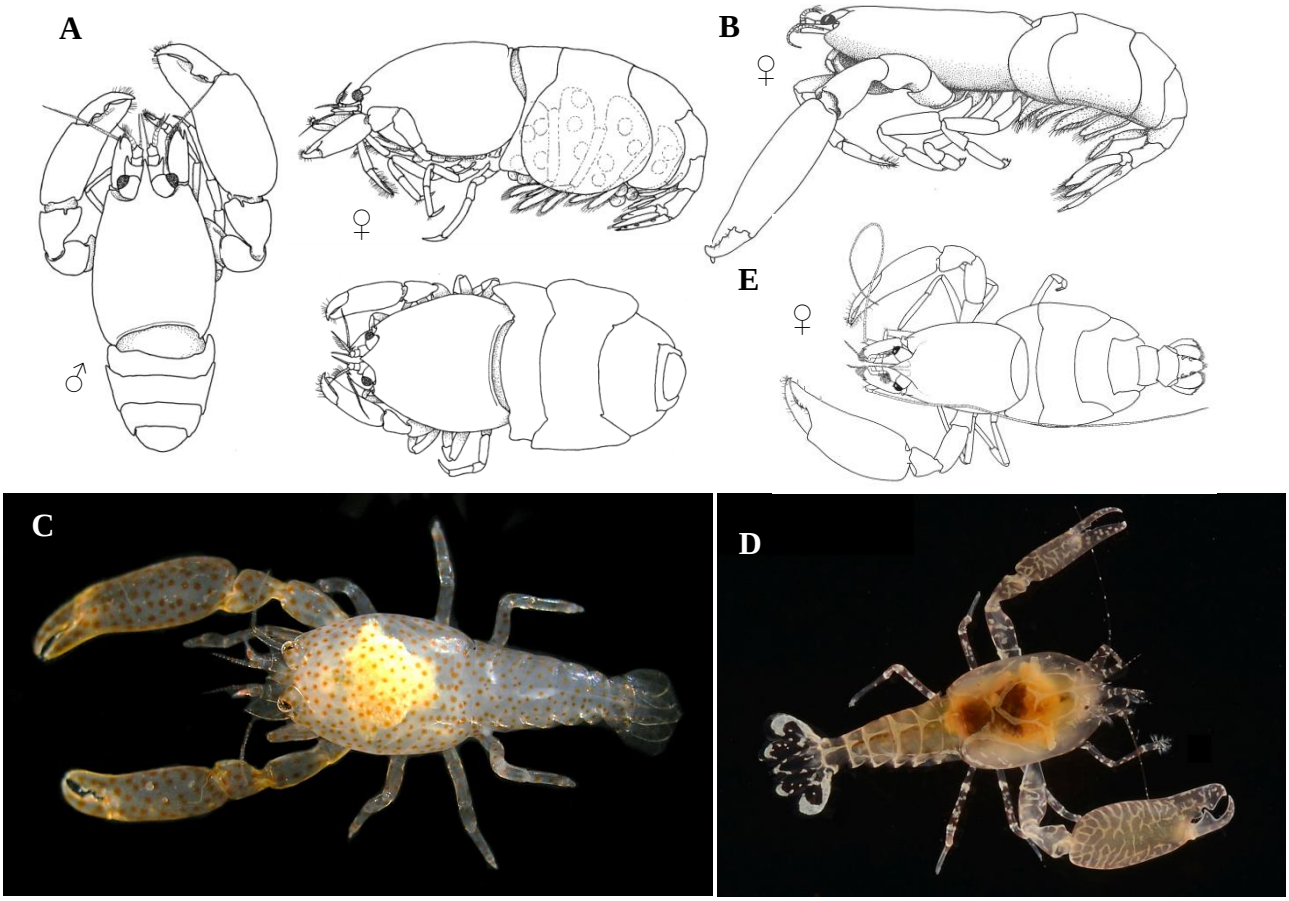


Figure 8. Body plans and coloration of mollusc- and ascidian-associated shrimps. Bivalve symbionts living inside host mantle cavities with a stout and swollen body form or greatly flattened body: A, *Conchodytes chadi* (Marin, 2011); B, *C. placunae* (Johnson, 1967); *C. meleagrinae* Peters, 1852; D, *Pontonia mexicana*. Ascidian symbionts living in branchial chamber: E, *Dactylonia ascidicola* (Borradaile, 1898). Figures A, B, E adopted from Marin (2011), Bruce (1995), Fransen (2002), respectively; photos by Z. Ďuriš.

4.5 Echinoderm-associated shrimps

Pontoniine shrimps associated with echinoderms (phylum Echinodermata) are represented by ectosymbiotic[1] forms living on external surface of all five major echinoderm classes, i.e., Crinoidea (feather stars), Ophiuroidea (brittle stars), Asteroidea (sea stars), Echinoidea (sea urchins), and Holothuroidea (sea cucumbers) (Bruce 1975).

Bruce (1982, 1995) reported the following genera among echinoderm-associated pontoniines: *Allopontonia* Bruce, 1972, *Araiopontonia* Fujino & Miyake, 1970, *Diapontonia* Bruce, 1986, *Laomenes* Clark, 1919, *Palaemonella* Dana, 1852, *Periclimenes*, *Pontoniopsis* Borradaile, 1915, *Stegopontonia* Nobili, 1906, *Tulеariocaris* Hipeau-Jacquotte, 1965, and *Zenopontonia*, with the most representatives in genus *Periclimenes* (which was, however, shown to be polyphyletic; e.g., Kou et al. 2013a; **Chapter 1**). Recently, new genera of shrimps associated with echinoderms, originally considered species complexes within *Periclimenes*, were subsequently separated from that genus. These include *Brucecaris* Marin & Chan, 2006, *Crinotonia* Marin, 2006, *Echinopericlimenes* Marin & Chan, 2014, *Lipkemenes* Bruce & Okuno, 2010, *Margitonia* Bruce, 2007, *Pontoniopsides* Bruce, 2005,

[1] One strange association was documented for *Conchodytes tridacnae* Peters, 1852. This species was found in the cloaca of holothurians although normally it is endosymbiont of bivalves of *Tridacna* Bruguière, 1797 (Bruce 1982).

Sandimenes Li, 2009, and *Unguicaris* Marin & Chan, 2006 (Marin 2006; Bruce 2005, 2007; Marin and Chan 2006, 2014; Li 2009; Bruce and Okuno 2010).

The majority of the above-mentioned genera are associated with sea urchins and crinoids in the tropical shallow waters, with the exception of the newly established deep-water genera *Echinopericlimenes* and *Bathymenes*, recorded from the depth up to 1280 m. The latter genus includes only one species *B. aleator* (Bruce, 1991) reported from echinoids, while the host of the majority of its congeners remains unknown (Marin and Chan 2014; Kou et al. 2015a). For the present time, only two pontoniine species, *Zenopontonia soror* (Nobili, 1904) and *Z. noverca* (Kemp, 1922), living exclusively on sea stars, and three species, *Periclimenes hongkongensis* Bruce, 1969, *P. pectiniferus* Holthuis, 1952 and *Z. rex* (Kemp, 1922), living on sea cucumbers. In the Indo-West Pacific, a single species, *Lipkemenes lanipes* (Kemp, 1922), is known as symbiont of the gorgonocephalid brittle stars (Bruce 1982).

Most shrimps associated with echinoderms are well adapted to live with these hosts that provide safe shelters, e.g., among or underneath long sharp and sometimes venomous sea-urchin spines or branched arms in crinoids (Bauer 2004). They often display specific morphology and coloration, or specific way of swimming. For instance, greatly specialized echinoid- associated genera living on spines (*Stegopontonia*, *Tuleariocaris*, Fig. 9A,B) are characterized by elongated body with unequal second pereiopods and short ambulatory legs bearing hooked biunguiculate dactyli used to cling on the host spines. Both also display specific moving behaviour when disturbed, swimming among spines with the head-down position similarly to the fish *Aeoliscus strigatus* (Günther, 1861) (Holthuis 1969; Bruce 1975). The second pereiopods are unequally developed and show great differentiation in the size and shape, they are also occur in other specialized shrimp genera, such as *Crinotonia* or *Pontoniopsis*, both crinoid-associated. On the other hand, '*Periclimenes*-like' echinoderm-associated species, e.g., *Allopontonia alastairi* Bruce, 2010 or *Palaemonella pottsi* (Borradaile, 1915), from sea urchins and crinoids, respectively, have light-built slender bodies with relatively long ambulatory legs bearing simple dactyli, and usually with subequal or moderately unequal second chelipeds (Bruce 1982, 1995).

The former 'gnathophyllid' shrimps are ecologically and morphologically very close to some traditional pontoniines, mainly to those associated with echinoderms. The echinoderm-associated 'gnathophyllids' are known within all their genera, except for the free-living species of the monotypic genus *Gnathophylleptum* Udekem d'Acoz, 2001 (Bruce 1982; Udekem d'Acoz 2001).

The surface tissue and mucus covering echinoderm body provide a good food source for their symbionts. Bruce (1975) and Bauer (2004) demonstrated that the shrimps' stomach is often observed to be full of material similar in colour to their host. The true relation to hosts nevertheless remains unknown although some indications show that the shrimps may be commensals scraping off food particles from host bodies (Bruce 1975; Marin 2006).

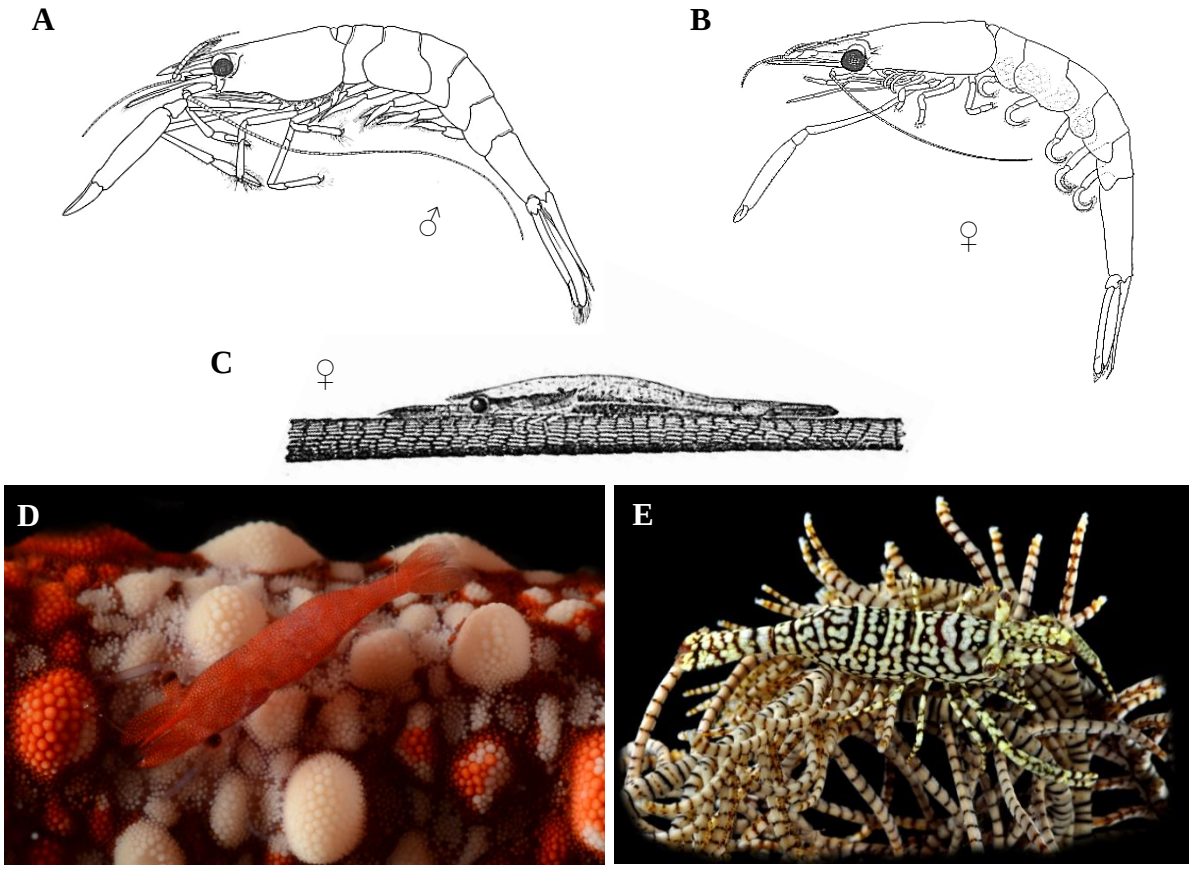


Figure 9. Echinoderm-associated palaemonid shrimps. Echinoid-associated species with elongated body adapted to living on the spines of diadematid sea urchins: A, *Stegopontonia commensalis*; B, *Tulеariocaris zanzibarica*; C, *T. neglecta*. D, starfish-associated *Zenopontonia soror*. E, crinoid-associated *Laomenes pardus* Marin, 2009. Figures A, B after Bruce (1995), figure C after Chace (1969); photos by Z. Ďuriš.

4.6 Fish-cleaning symbioses

In general, the cleaning symbiosis is defined as relationship in which cleaner remove ectoparasites, diseased tissue or unwanted food particles from apparently cooperating client that visits the cleaner. The term 'cleaning symbiosis', however, is used for the interactions limited to only few seconds or minutes while the general term 'symbiosis' is often used for animals living together for longer time. The cleaning relation is mutualistic, the cleaner obtains a food and the client is freed from parasites (e.g., Floeter et al. 2007; Feder 1966; Bauer 2004). Bshary et al. (2007) confirmed the benefits for the client also by demonstrating that cortisol levels were reduced in holding-water of client. On the other hand, according to Grutter (2000) or Cheney and Côté (2005), the cleaning interactions may be mutualistic at some sites, but neutral or even parasitic at others, depending on the quantity of ectoparasites. The cleaning symbiosis was documented for different marine animals, but especially for fishes and shrimps as cleaners, with the clients being predominantly fish. The cleaner shrimps occur mainly in the tropical regions at specific sites commonly known as cleaning stations (Feder 1966; Limbaugh et al. 1961); less frequently they were observed also in temperate waters (Östlund-Nilsson et al. 2005). In shrimps, the cleaning symbiosis was observed only in some species of the infraorders Caridea and Stenopodidea (e.g., Bruce 1976b), in the latter only one species, *Stenopus hispidus*, is involved in cleaning symbioses with fishes, but also with hawksbill turtles (Sazima et al. 2004).

Wicksten (2009), following Limbaugh et al. (1961) and Bauer (2004), summarized the features which are consistently present in most shrimps considered cleaners: (1) Distinctive pattern of

contrasting colours, including white antennae and often a white mid-dorsal line or white appendages; (2) Characteristic soliciting behaviour: twitching the antennae or rocking the body on approach of a client fish; (3) Reciprocal activity patterns of the client fish: orienting the body toward the shrimp, puffing the gills, extending the fins, changing colour or orienting nose down; (4) Remaining in a cleaning station – a particular hole, or host sea anemone – over time; (5) Diurnal activity.

Only some species of five genera of palaemonid shrimps (*Ancylomenes*, *Brachycarpus*, *Palaemon*, *Periclimenes*, *Urocaridella*) were observed in cleaning interaction with fishes (Fig. 10); some of them were observed repeatedly, others only occasionally. Complying the required features mentioned above for habitats, colour patterns and behaviour, only the members of genera *Ancylomenes* (6 species), *Periclimenes* (1 species), and *Urocaridella* (3 species), can be suggested true cleaners among palaemonids. For two species, *A. holthuisi* (Fig. 10B) and *A. magnificus*, the fish-cleaning was predicted based on distinctive advertising of the cleaning services, i.e. rapid waving of chelipeds, sideward swinging body movement, or swaying-style of swimming (e.g., Becker and Grutter 2005; Chadwick et al. 2008; Chapuis and Bshary 2010; Huebner and Chadwick 2012; **Chapter 2**). The remaining taxa, i.e., *Brachycarpus biunguiculatus* with nocturnal activity (Bauer 2004) and two *Palaemon* species, were observed as occasionally cleaners (e.g., Östlund-Nilsson et al. 2005), but their morphology, colouration and behaviour are quite different from above-mentioned palaemonid cleaners.

Our phylogenetic analysis including 14 cleaner palaemonid species from all those genera confirmed a parallel evolution of cleaning behaviour in five separate lineages, within Palaemonidae. Our results points to remarkable morphological, colour and behavioural convergence in two lineages of the actual *Ancylomenes* spp. and suggest that these characteristics may be facilitated by communication with fish clients (**Chapter 2**).

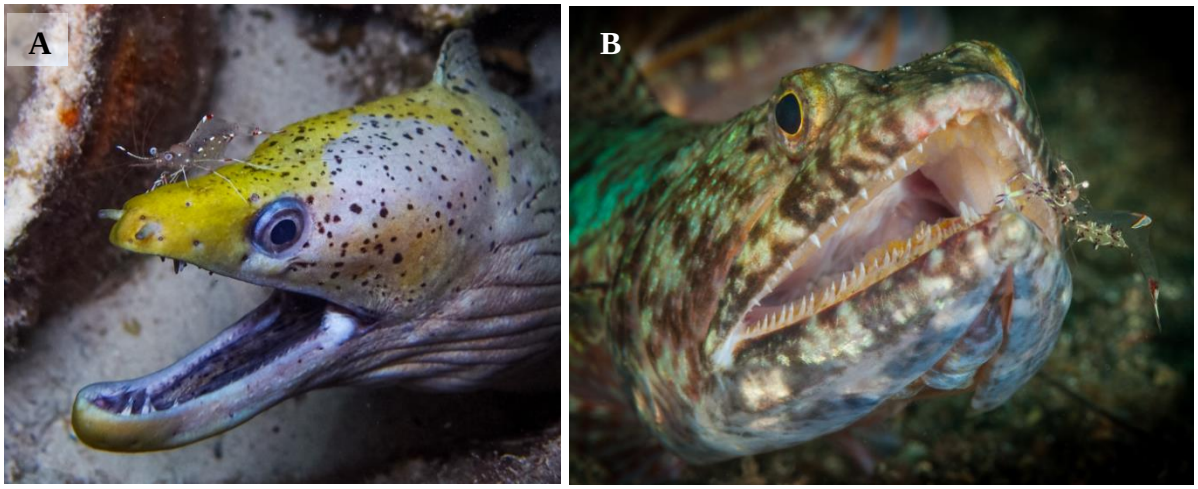


Figure 10. Indo-West Pacific fish-cleaning palaemonid shrimps. A, *Urocaridella pulchella* Yokes & Galil, 2006 on the fimbriated moray eel; B, *Ancylomenes holthuisi* (Bruce, 1969) on the lizardfish; photos with permission from Shutterstock.

4.7 Host-switching in pontoniine shrimps

The host-switching (colonization of the new host) is together with coadaptation and cospeciation considered one of the main drivers of speciation and plays a key role in diversification of symbiotic forms (Goto et al. 2012, 2014). Several studies demonstrated that host associations are generally conserved across phylogenies and that switches between distantly related hosts are infrequent (e.g., Hoberg and Brooks 2008; Gómez et al. 2010). The majority of studies so far dealt

with terrestrial ecosystems and little is known about how symbiotic organisms expand and colonise the new hosts in the marine environments (Goto et al. 2012).

Palaemonidae with the highest share of symbiotic species within caridean family is rarely mentioned with connection to the host switching. Only limited information about switching of shrimps between hosts of different phyla was reported in earlier studies. For example, Fransen and Goud (2000) observed *Zenopontonia rex* (Kemp, 1922) living on sea-stars as well as on nudibranchs, or Marin and Anker (2008) found shrimp *Pontonia panamica* inside ascidian host and suggested; latter authors suggested, based on phylogeny provided by Fransen (2002), that the host switching from Ascidiacea to Mollusca developed relatively early in the evolutionary history of this genus.

Recently, Kou et al. (2015b) or Gan et al. (2015a) provided some insights into the evolution of pontoniine symbioses with discussion of host-switching; both studies are based on limited data sets including only Indo-West Pacific taxa. Kou et al. (2015b) identified divergent evolutionary pathways in symbiotic shrimps using molecular data, and suggested that symbiotic pontoniines can be divided into two major clades composed of two groups, the 'primitive' and 'derived' groups, both supported also morphologically. Gan et al. (2015a), in accordance with Kou et al. (2015b), confirmed that cnidarian, echinoderm or ascidian associations evolved multiple times within Palaemonidae.

The switching between hosts is relatively common within phylum, but it occurs, probably much more frequently than was previously assumed, also among host phyla (Goto et al. 2012, 2014; Kou et al. 2015b). The last contribution to this topic is a part of my PhD thesis (**Chapter 1**).

Conclusions

Based on phylogeny and ancestral state analysis we confirmed that colonisations of the new hosts via the host-switching events played the major role in evolution of palaemonid symbiotic shrimps and led to implementation of new body plans and ecological adaptations. Our results also showed that occurrence of the inter-phylum host switching, together with switches from ecto- to endosymbiotic mode of life, evolved multiple times in palaemonid evolution while the reversal back to a free-living mode of life is a rare phenomenon, only occasionally observed among ectosymbiotic lineages. Among other, the reconstructed phylogeny of symbiotic palaemonids has provided also an array of questions requiring further systematic re-arrangements. We indicated several poly- or paraphyletic genera, e.g., the pantropical *Periclimenes* or *Cuapetes* containing predominantly free-living representatives. Based on the initial results presented in this PhD thesis, the two last-mentioned mentioned genera are the objects of two newly launched PhD projects at the University of Ostrava.

The cleaning symbioses of palaemonid shrimps representing a special type of interactions are documented particularly in tropical regions. The shrimps play the role as cleaners and often perform specific behavioural signals to attract fish clients. Based on phylogenetic analysis including fish-cleaning shrimps from genera *Ancylomenes*, *Brachycarpus*, *Palaemon* and *Urocaridella*, we confirmed five independent lineages of the fish-cleaning symbiosis within Palaemonidae. In two unrelated lineages of anemone associated shrimps (Indo-West Pacific *Ancylomenes* spp. and western Atlantic *Ancylomenes*/*Periclimenes* spp.) we demonstrated their striking parallelisms in the general body shape, colour patterns and fish-attracting behaviour. We confirmed their remote and unrelated position on the phylogenetic background as well, and we assume that this parallel evolution of mentioned morphological patterns and behaviour reflects an adaptation to the fish-cleaning symbiosis followed with similar modes of communication with fish hosts (clients).

The symbiotic relations between shrimps and their hosts are well-known but true nature of these relations is feebly explored. The analysis of stomach contents is one way how to exactly recognize at least the trophic relations and impact of symbionts to their host. Based on our results with sponge-dwelling shrimps in the Caribbean Sea, we proved that endosymbionts (i.e., palaemonid and alpheid shrimps) are in most cases parasites of their hosts, and we suggest that similar detailed studied will uncover parasitic relations between many other symbiotic shrimps and their hosts. Similarly, detailed examination of the morphology of main claws in *Typton* species revealed adaptations reflecting their parasitic mode of feeding. Their claws are strongly shear-like, and bear traces of intensive shearing of sponge host tissues.

Within my thesis, I contributed to description of seven new species of shrimps using morphological and molecular evidences. These new taxa include the Indo-West Pacific or Atlantic representatives of Palaemonidae, Alpheidae and Pandalidae. With the exception of two species, all of the new shrimps live symbiotically with their cnidarian or sponge hosts. Such new descriptions are likely only the ”tip of the iceberg” of diversity yet to be discovered among symbiotic marine crustaceans.

References

Huebner, L.K., Chadwick, N.E., 2012. Patterns of cleaning behaviour on coral reef fish by the anemoneshrimp *Ancylomenes pedersoni*. *Journal of the Marine Biological Association of the United Kingdom*, 92: 1557-1562.

Becker, J.H.A., Grutter, A.S., 2005. Client fish ectoparasite loads and cleaner shrimp *Urocaridella* sp. c hunger levels affect cleaning behaviour. *Animal Behaviour* 70(5): 991–996.

Bshary, R., Oliveira, R.F., Oliveira, T.S., Canário, A.V., 2007. Do cleaning organisms reduce the stress response of client reef fish? *Frontiers in Zoology* 4(1): 21.

Abele, L.G., Felgenhauer, B.E., 1982. Decapoda. In: S.P. Parker (ed.): Synopsis and classification of living organisms. McGraw-Hill Book Co., New York, 296–326.

Anker, A., Ahyong, S.T., Noël, P., Palmer, A.R., 2006. Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution* 60(12): 2507–2528.

Anker, A., Hurt, C., Knowlton, N., 2007. Three transisthmian snapping shrimps (Crustacea: Decapoda: Alpheidae: *Alpheus*) associated with innkeeper worms (Echiura: Thalassematidae) in Panama. *Zootaxa* 1626: 1–23.

Anker, A., Hurt, C., Knowlton, N., 2009. Description of cryptic taxa within the *Alpheus bouvieri* A. Milne-Edwards, 1878 and *A. hebes* Kim and Abele, 1988 species complexes (Crustacea: Decapoda: Alpheidae). *Zootaxa* 2153: 1–23.

Anker, A., Jeng, M.-S., Chan, T.-Y., 2001. Two unusual species of Alpheidae (Decapoda: Caridea), associated with upogebiid mudshrimps in the mudflats of Taiwan and Vietnam. *Journal of Crustacean Biology* 21: 1049–1061.

Anker, A., Komai, T., Marin, I.N., 2015. A new echiuran-associated snapping shrimp (Crustacea: Decapoda: Alpheidae) from the Indo-West Pacific. *Zootaxa* 3914(4): 441–455.

Anker, A., Marin, I., 2007. *Athanas anatidactylus* n. sp., a new alpheid shrimp associated with crinoids in the tropical western Pacific (Crustacea: Decapoda). *Zoological Studies* 46: 162–167.

Ayón-Parente, M., Hendrickx, M.E., Galvan-Villa, C.M., 2015. A new species of the genus *Typton* Costa (Crustacea: Decapoda: Palaemonidae: Pontoniinae) from the eastern tropical Pacific. *Zootaxa* 3926(3): 430–438.

Baeza, J.A., 2008. Social monogamy in the shrimp *Pontonia margarita*, a symbiont of Pinctada mazatlanica, off the Pacific coast of Panama. *Marine Biology* 153: 387–395.

Baeza, J.A., Bolaños, J.A., Hernandez, J.E., Lira, C., Lopez, R., 2011. Monogamy does not last long in *Pontonia mexicana*, a symbiotic shrimp of the amber pen-shell *Pinna carnea* from the southeastern Caribbean Sea. *Journal of Experimental Marine Biology and Ecology* 407: 41–47.

Baeza, J.A., Díaz-Valdés, M., 2011. The symbiotic shrimp *Ascidonia flavomaculata* lives solitarily in the tunicate *Ascidia mentula*: implications for its mating system. *Invertebrate Biology* 130: 351–361.

Baeza, J.A., Hemphill, C.A., Ritson-Williams, R., 2015. The Sexual and Mating System of the Shrimp *Odontonia katoi* (Palaemonidae, Pontoniinae), a Symbiotic Guest of the Ascidian *Polycarpa aurata* in the Coral Triangle. *PLoS ONE* 10(3): e0121120.

Baeza, J.A., Ritson-Williams, R., Fuentes, M.S., 2013. Sexual and mating system in a caridean shrimp symbiotic with the winged pearl oyster in the Coral Triangle. *Journal of Zoology* 289(3): 172–181.

Baeza, J.A., Thiel, M., 2007. The mating system of symbiotic crustaceans. A conceptual model based on optimality and ecological constraints. Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms, 250–267.

Bauer, T., 2004. Remarkable Shrimps: Adaptations and Natural History of the Carideans. Animal Natural History Series, volume 7. University of Oklahoma Press, 296 pp.

Boxshall, G., Jaume, D., 2013. Antennules and antennae in the Crustacea. In: The Natural History of the Crustacea, Functional Morphology & Diversity, Watling L. & Thiel M. (eds), vol. 1: 199–236.

Bracken, H.D., De Grave, S., Felder, D.L., 2009. Phylogeny of the infraorder Caridea based on mitochondrial and nuclear genes (Crustacea: Decapoda). In: Decapod crustacean phylogenetics Martin J.W., Crandal K.A., Feder D.L. (eds), *Crustacen Issue* 18: 281–305.

Bruce, A.J., 1969. Notes on Some Indo-Pacific Pontoniinae. XIV. Observations on *Paratypton siebenrocki* Balss. *Crustaceana* 17(2): 171–186.

Bruce, A.J., 1972. Shrimps that live with molluscs. *Sea Frontiers* 18: 218–227.

Bruce, A.J., 1975. Shrimps that live with echinoderms. *Sea Frontiers* 21(1): 44–53.

Bruce, A.J., 1976a. Shrimps and prawns of coral reefs, with special reference to commensalism. *Biology and Geology of Coral Reefs* (3): 37–94.

Bruce, A.J., 1976b. Coral reef Caridea and "commensalism". *Micronesica* 12(1): 83–98.

Bruce, A.J., 1977. The hosts of the coral-associated Indo-West-Pacific Pontoniine shrimps. *Attol Research Bulletin* 205: 1–19.

Bruce, A.J., 1982. The shrimps associated with Indo-West Pacific echinoderms, with the descriptions of a new species in the genus *Periclimenes* Costa, 1844 (Crustacea: Pontoniinae) 16: *Memoirs-The Australian Museum* 191–216.

Bruce, A.J., 1983. *Miropandalus hardingi*, new genus, new species, a bizarre commensal pandalid shrimp from the Marshall Islands. *Journal of Crustacean Biology* 3: 482–490.

Bruce, A.J., 1985. The shrimps of tropical seas. *Northern Territory Naturalist* (8): 18–27.

Bruce, A.J., 1986. Observations on the family Gnathophyllidae Dana, 1852 (Crustacea: Decapoda). *Journal of Crustacean Biology* 6(3): 463–470.

Bruce, A.J., 1988. A note on the first zoeal stage larva of *Hymenocera picta* Dana (Crustacea: Decapoda: Palaemonidae). *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 5(1): 119–124.

Bruce, A.J., 1991. A second occurrence of the bizarre shrimp *Miropandalus hardingi* (Crustacea: Decapoda: Pandalidae). *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 8: 11–14.

Bruce, A.J., 1995. A synopsis of the Indo-West Pacific genera of the Pontoniinae (Crustacea: Decapoda: Palaemonidae). *Theses Zoologicae* 25: 172 pp. Königstein, Koeltz Scientific Books, R. Fricke (ed.)

Bruce, A.J., 2005. A new genus *Pontoniopsides*, for *Pontoniopsis paulae* Gore, 1981 (Crustacea: Decapoda: Pontoniinae). *Zootaxa* 826: 1–4.

Bruce, A.J., 2007. A re-definition of the genus *Periclimenes* Costa, 1844 and the designation of a new genus *Margitonia* (Crustacea: Decapoda: Pontoniinae). *Cahiers de Biologie Marine* 48(4): 403–406.

Bruce, A.J., 2008. *Periclimenes aqabai* sp. nov, a further species of the *aesopius* species group (Caridea: Pontoniinae) from the Red Sea. *Zootaxa* 1682: 27–32.

Bruce, A.J., 2013. *Ancylomenes australis* sp. nov. (Crustacea: Decapoda: Pontoniinae) from South Africa. *Zootaxa* 3722(1): 73–82.

Bruce, A.J., Okuno, J., 2006. *Periclimenes dardanicola* n. sp., a new species of hermit crab associated shrimp (Crustacea, Decapoda, Palaemonidae) from the western Pacific. *Zoosystema* 28(2): 367–377.

Bruce, A.J., Okuno, J., 2010. Designation of a new genus *Lipkemenes*, with supplementary description and range extension of its type species, *L. lanipes* (Kemp, 1922) (Decapoda, Palaemonidae). *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume. Crustaceana Monographs* 14: 159–171.

Bruce, A.J., Svoboda, A., 1983. Observations upon some Pontoniine Shrimps from Aqaba, *Jordan*. *Zoologische Verhandelingen.* 205: 1–44.

Burkenroad, M.D., 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Studies in Geology* 2(1): 1–17.

Chace, F.A. Jr., 1985. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907-1910, Part 3: Families Thalassocarididae and Pandalidae. *Smithsonian Contributions to Zoology* 411: 1–143.

Chace, F.A. Jr., 1992. On the classification of the Caridea (Decapoda). *Crustaceana* 63: 70–80.

Chace, F.A. Jr., Bruce, A.J., 1993. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition 1907–1910, Part 6: Superfamily Palaemonoidea. *Smithsonian Contributions to Zoology* 543:1–152.

Chadwick, N., Ďuriš, Z., Horká, I., 2008. Biodiversity and behavior of shrimps and fishes symbiotic with sea anemones in the Gulf of Aqaba, northern Red Sea. In: Por D.V., Ben-Eliahu N. (eds), *High Biodiversity of the Gulf of Aquaba*, Magnes Press, 209–225.

Chapuis, L., Bshary, R., 2010. Signalling by the cleaner shrimp *Periclimenes longicarpus*. *Animal Behaviour*, 79: 645–647.

Cheney, K.L., Côté, I.M., 2005. Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biology Letters*, 1(2): 162–165.

Christoffersen, M.L., 1988. Phylogenetic systematics of the Eucarida (Crustacea Malacostraca). *Revista Brasileira de Zoologia* 5(2): 325–351.

Criales, M.M., 1979. Ecologia y etologia de los camarones limpiadores de peces *Periclimenes pedersoni* y *Lysmata grabhami*, en la bahia de Santa Marta. *Acta Cientifica Venezolana* 30: 570–576.

Criales, M.M., 1984. Shrimps associated with Coelenterates, Echinoderms, and Molluscs in the Santa Marta region, Columbia. *Journal of Crustacean Biology* 4(2): 307–317.

De Grave, S., 2001. Biogeography of Indo-Pacific Pontoniinae (Crustacea, Decapoda): a PAE analysis. *Journal of Biogeography* 28: 1239–1253.

De Grave, S., Cai, Y., Anker, A., 2008. Global diversity of shrimps (Crustacea: Decapoda: Caridea) in freshwater. *Hydrobiologia* 596(1): 287–293.

De Grave, S., Pentcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Wetzer, R., 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*, Suppl. 21: 1-109.

De Grave, S., Fransen, C.H.J.M., 2011. Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen, Leiden* 85: 195–589.

De Grave, S., Fransen, C.H.J.M., Page, T.J., 2015. Let's be pals again: major systematic changes in Palaemonidae (Crustacea: Decapoda). *PeerJ* 3: e1167.

De Grave, S., Li, C.P., Tsang, L.M., Chu, K.H., Chan, T.-Y., 2014. Unweaving hippolytoid systematics (Crustacea, Decapoda, Hippolytidae): resurrection of several families. *Zoologica Scripta* 43: 496–507.

Debelius, H., 1999. Crustacea Guide of the World: Atlantic Ocean, Indian Ocean, Pacific Ocean. IKAN-Unterwasserarchiv, 321 pp.

Dobson, N.C., De Grave, S., Johnson, M.L., 2014. Linking eye design with host symbiont relationships in pontoniine shrimps (Crustacea, Decapoda, Palaemonidae). *PLoS ONE 9*: e99505.

Duffy, J. E., Macdonald, K. S., 1999. Colony structure of the social snapping shrimp *Synalpheus filidigitus* in Belize. *Journal of Crustacean Biology 19*(2): 283–292.

Duffy, J. E., Morrison, C. L., 2000. Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). *Evolution* 54(2): 503–516.

Duffy, J.E., 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. *Marine ecology progress series* 90: 127–138.

Duffy, J.E., 1996. Eusociality in a coral-reef shrimp. *Nature* 381: 512–514.

Ďuriš, Z., Anker, A., 2014. *Athanas manticolus* sp. nov., a new stomatopod-associated alpheid shrimp from Vietnam (Crustacea, Decapoda). *Zootaxa* 3784 (5): 550–558.

Ďuriš, Z., Bruce, A.J., 1995. A revision of the 'petitthouarsii' group of species of the genus *Periclimenes* Costa (Crustacea: Decapoda: Palaemonidae). *Journal of Natural History* 29: 619–671.

Fautin, D.G., Guo, C.-C., Hwang, J.-S. 1995. Costs and benefits of the symbiosis between the anemoneshrimp *Periclimenes brevicarpalis* and its host *Entacmaea quadricolor*. *Marine Ecology Progress Series* 129: 77–84.

Feder, H.M., 1966. Cleaning symbiosis in the marine environment. In: Symbiosis. Henry, S.M. (ed.) 327–380.

Floeter, S.R., Vázquez, D.P., Grutter, A.S., 2007. The macroecology of marine cleaning mutualisms. *Journal of Animal Ecology* 76(1): 105–111.

Fransen, C.H.J.M, van der Meij, S.E., 2010. First record of a pontoniine shrimp (Caridea, Palaemonidae) in association with a boring bivalve of the genus *Spengleria* (Bivalvia, Euheterodonta, Gastrochaenidae). *Crustaceana* 83(11): 1391–1400.

Fransen, C.H.J.M., 2002. Taxonomy, phylogeny, historical biogeography, and historical ecology of the genus *Pontonia* (Crustacea: Decapoda: Caridea: Palaemonidae). *Zoologische Verhandelingen, Leiden* 336: 1–433.

Fransen, C.H.J.M., 2003. *Poripontonia dux* gen. nov., spec. nov., a sponge associated shrimp (Crustacea, Decapoda, Caridea, Palaemonidae, Pontoniinae) from Indonesia. *Zoologische Verhandelingen, Leiden* 345: 129–138.

Fransen, C.H.J.M., 2006. On Pontoniinae (Crustacea, Decapoda, Palaemonidae) collected from ascidians. *Zoosystema* 28: 713–746.

Fransen, C.H.J.M., Goud, J., 2000. *Chromodoris magnifica* (Quy & Gaimard, 1832), a new nudibranch host for the shrimp *Periclimenes imperator* Bruce, 1967 (Pontoniinae). *Zoologische Mededelingen, Leiden* 73(18): 273–283.

Fransen, C.H.J.M., Reijnen, B.T., 2012. A second discovery of *Lacertopontonia chadi* Marin, 2011 (Crustacea: Decapoda: Palaemonidae), with remarks on its systematic position. *Zootaxa* 3437: 43–50.

Fujino,T., Takeda, M., 1977. *Levicaris mammillata* (Edmonson), a gnathophyllid shrimp associated with slate-pencil sea urchin, *Heterocentrotus mammillatus* (Linnaeus), from the Ogasawara and Ryukyu Islands. *Bulletin of the National science Museum, Series A (Zoology)* 3(3): 131–140.

Gan, Z.B., Li, X., Chan, T.-Y., Chu, K.H., Kou, Q., 2015a. Phylogeny of Indo-West Pacific pontoniine shrimps (Crustacea: Decapoda: Caridea) based on multilocus analysis. *Journal of Zoological systematics and Evolutionary Research* 53(4): 282–290.

Gan, Z.B., Li X.., Kou, Q., Chan, T.-Y., Chu, K.H., Huang, H., 2015b. Systematic status of the caridean families Gnathophyllidae Dana and Hymenoceridae Ortmann (Crustacea: Decapoda): a further examination based on molecular and morphological data. *Chinese Journal of Oceanology and Limnology* 33(1): 149–158.

Gómez, J. M., Verdú, M., Perfectti, F., 2010. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* 465: 918–921.

Goto, R., Kawakita, A., Ishikawa, H., Hamamura, Y., Kato, M., 2012. Molecular phylogeny of the bivalve superfamily Galeommatoidea (Heterodonta, Veneroida) reveals dynamic evolution of symbiotic lifestyle and interphylum host switching. *BMC Evolutionary Biology* 12: 172.

Goto, R., Ishikawa, H., Hamamura, Y., Sato, S. I., Kato, M., 2014. Evolution of symbiosis with *Lingula* (Brachiopoda) in the bivalve superfamily Galeommatoidea (Heterodonta), with description of a new species of Koreamya. *Journal of Molluscan Studies* 80(2): 148–160.

Gunn, A., Pitt, S.J., 2012. Parasitology: an integrated approach. John Wiley & Sons, 442 pp.

Guo, C.C., Hwang, J.S. and Fautin D.G. 1996. Host selection by shrimps symbiotic with sea anemones: A field survey and experimental laboratory analysis. *Journal of Experimental Marine Biology and Ecology* 202: 165–176.

Grutter, A.S., 2000. Cleaner fish really do clean. *Nature* 398: 672–673.

Hayashi, K. I., 2002. A new species of the genus *Athanas* (Decapoda, Caridea, Alpheidae) living in the burrows of a mantis shrimp. *Crustaceana*, 75(3): 395–403.

Hayashi, K.I., 1975. *Anachlorocurtis commensalis* gen. nov., sp. nov. (Crustacea, Decapoda, Pandalidae), a new pandalid shrimp associated with antipatharian corals from central Japan. *Annotationes Zoologicae Japonenses* 48: 172–182.

Hayashi, K.I., 1988. Species status of *Pandalus gracilis* (Decapoda, Caridea, Pandalidae). *Nippon Suisan Gakkaishi* 54(1): 71–75.

Hoberg, E.P., Brooks, D.R. A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host-parasite systems. *Journal of Biogeography* 35: 1533–1550.

Holthuis, L.B., 1951. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchidae and Pontoniinae. I: The subfamilies Euryrhynchinae and Pontoniinae. Allan Hancock Foundation Publications, Occasional Paper 11: 1–332, 63 pls.

Holthuis, L.B., 1980. FAO Species Catalogue. Vol. 1 - Shrimps and Prawns of the World. An Annotated Catalogue of Species of Interest to Fisheries. *FAO Fisheries Synopsis* 125(1): i–xvii, 1–271.

Holthuis, L.B., 1993. The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda): with an appendix on the order Amphionidacea. National Natuhrhistorisch Museum, Leiden, 328 pp.

Hultgren, K. M., Hurt, C., Anker, A., 2014. Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). *Molecular phylogenetics and evolution* 77: 116–125.

Hultgren, K., Macdonald, K.S., Duffy, J.E., 2010. Sponge-dwelling snapping shrimps of Curaçao, with descriptions of three new species. *Zootaxa* 2372: 221–262.

Hurt, C., Silliman, K., Anker, A., Knowlton, N., 2013. Ecological speciation in anemone-associated snapping shrimps (*Alpheus armatus* species complex). *Molecular Ecology* 22: 4532–4548.

Johnson, D.S., 1967. On some commensal decapod crustaceans from Singapore (Palaemonidae and Porcellanidae). *Journal of Zoology, London* 153: 499–526.

Johnson, D.S., Liang, M., 1966. On the biology of the Watchman prawn, *Anchistus custos* (Crustacea; Decapoda; Palaemonidae), an Indo-West Pacific commensal of the bivale *Pinna*. *Journal of Zoology*, 150(4): 433–435.

Karplus, I., 1987. The association between gobiid fishes and burrowing alpheid shrimps. *Oceanography and Marine Biology Annual Review* 25: 507–562.

Karplus, I., Szlep, R., Tsurnamal, M., 1981. Goby-shrimp partner specificity. I. Distribution in the northern Red Sea and partner specificity. *Journal of Experimental Marine Biology and Ecology* 51(1): 1–19.

Karplus, I., Thompson, A.R., 2011. The partnership between gobiid fishes and burrowing alpheid shrimps. *Biology of gobies. Science Publishers, Inc., New Hampshire*, 559–608.

Kemp, S., 1922. Notes on Crustacea Decapoda in the Indian Museum, XV. Pontoniinae. *Records of the Indian Museum* 24: 113–288, Plates 1–9.

Knowlton, N., Keller, B.D., 1985. Two more sibling species of alpheid shrimps associated with the Caribbean sea anemones *Bartholomea annulata* and *Heteractis lucida*. *Bulletin of Marine Science* 37(3): 893–904.

Komai, T., Eletskaya, M., 2008. A new species of the pandalid shrimp genus *Pandalus* (Crustacea: Decapoda: Caridea) from the Sea of Okhotsk off eastern Sakhalin, Russian Far East. *Zootaxa* 1882: 46–56.

Kou, Q., Li, X., Bruce, A.J., 2015a. Designation of a new genus *Bathymenes* for the deep-sea pontoniine shrimps of the *Periclimenes alcocki* species group (Decapoda, Caridea, Palaemonidae), with a checklist of the species assigned to the genus. *Chinese Journal of Oceanology and Limnology* 34: 170–176.

Kou, Q., Li, X. Z., Chan, T. Y., Chu, K. H., 2015b. Divergent evolutionary pathways and host shifts among the commensal pontoniine shrimps: a preliminary analysis based on selected Indo-Pacific species. *Organisms Diversity & Evolution* 15(2): 369–377.

Kou, Q., Li, X., Chan, T.-Y., Chu, K.H., Gan, Z., 2013b. Molecular phylogeny of the superfamily Palaemonoidea (Crustacea: Decapoda: Caridea) based on mitochondrial and nuclear DNA reveals discrepancies with the current classification. *Invertebrate systematics* 27(5): 502–514.

Kou, Q., Li, X., Chan, T.-Y., Chu, K.H., Huang, H., Gan, Z., 2013a. Phylogenetic relationships among genera of the *Periclimenes* complex (Crustacea: Decapoda: Pontoniinae) based on mitochondrial and nuclear DNA. *Molecular Phylogenetics and Evolution* 68: 14–22.

Li, X. , 2009. *Sandimenes* nov. gen., for *Periclimenes hirsutus* Bruce, 1971 (Decapoda, Caridea, Pontoniinae). *Crustaceana* 82(7): 881–896.

Li, X., Bruce, A.J., 2006. Further Indo-West Pacific palaemonoid shrimps (Crustacea: Decapoda: Palaemonoidea), principally from the New Caledonian region. *Journal of Natural History* 40: 611–738.

Li, X.Z., Liu, R.Y., Liang X.Q., 2003. The zoogeography of Chinese Palaemonoidea fauna. *Biodiversity Science* 11: 393–406.

Limbaugh, C., Pederson, H., Chace, Jr. F.A., 1961. Shrimps that clean fishes. *Bulletin of Marine Science of the Gulf and Caribbean* 11: 237–257.

Lohse, D., Schmitz, B., Versluis, M., 2001. Snapping shrimp make flashing bubbles. *Nature* 413(4): 477–478.

Marin, I. N., Chan, T.-Y., 2006. Two new genera and a new species of crinoid-associated pontoniine shrimps (Decapoda: Caridea: Palaemonidae). *Journal of Crustacean Biology* 26(4): 524–539.

Marin, I., 2006. Description of *Crinotonia anastasiae*, new genus, new species, a new crinoid associated pontoniine shrimp (Crustacea: Caridea) from Nha Trang Bay, Vietnam, with inclusion of *Periclimenes attenuatus* Bruce, 1971, in the new genus. *The Raffles Bulletin of Zoology* 54: 321–340.

Marin, I., 2007. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) inhabiting boring sponges (Porifera: Demospongia) from Nhatrang Bay, Vietnam, with descriptions of three new species. *Zoologische Mededelingen, Leiden* 81: 217–240.

Marin, I., 2010. On the presence of the symbiotic alpheid shrimp *Aretopsis amabilis* in the coastal waters of Nhatrang Bay, Vietnam. *Marine Biodiversity Records* 3: e74 (4 pp.)

Marin, I., 2011. *Lacertopontonia chadi* gen. et sp. nov., a new oyster-associated *Pontonia*-like pontoniine shrimp (Crustacea, Decapoda, Palaemonidae) from the Great Barrier Reef of Australia. *Zootaxa* 2968: 57–68.

Marin, I., 2015. New records of pontoniine shrimp genus *Onycocaris* Nobili, 1904 (Crustacea: Decapoda: Palaemonidae) from the Indo-Pacific with the description of two new species from French Polynesia. *Arthropoda Selecta* 24(3): 283–302.

Marin, I., Anker, A., 2008. A new species of *Pontonia* Latreille, 1829 (Crustacea, Decapoda, Palaemonidae) associated with sea squirts (Tunicata, Ascidiacea) from the Pacific coast of Panama. *Zoosystema* 30(2): 501–515.

Marin, I., Chan, T.-Y., 2013. *Typtonomenaeus formosanus* gen. et sp. nov., a new sponge-associated pontoniine shrimp (Crustacea: Decapoda: Palaemonidae: Pontoniinae) from northern Taiwan. *Zootaxa* 3664(1): 45–56.

Marin, I., Chan, T.-Y., 2014. Deep water echinoid-associated pontoniine shrimp "*Periclimenes hertwigi* Balss, 1913" species group (Crustacea: Decapoda: Caridea: Palaemonidae): species review, description of a new genus and species from Philippines. *Zootaxa* 3835: 301–324.

Marin, I., Paulay, G., 2010. *Pinnotherotonia rumphiusi* gen. et sp. nov., a new furry bivalve-associated pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from Palau. *Zootaxa* 2636: 37–48.

Mitsuhashi, M., Sin, Y.W., Lei, H.C., Chan, T.-Y., Chu, K.H., 2007. Systematic status of the caridean families Gnathophyllidae Dana and Hymenoceridae Ortmann (Crustacea: Decapoda): a preliminary examination based on nuclear rDNA sequences. *Invertebrate Systematics* 21: 613–622.

Moore, R.C., 1969. Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 2. Geological Society of America and University of Kansas, Lawrence, R400-R651.

Okuno, J., Bruce, A.J., 2010. Designation of *Ancylomenes* gen. nov., for the '*Periclimenes aesopius* species group' (Crustacea: Decapoda: Palaemonidae), with the description of a new species and a checklist of congeneric species. In: De Grave, S. & Fransen, C.H.J.M. (2010) Contributions to shrimp taxonomy. *Zootaxa* 2372: 1–414.

Östlund-Nilsson, S., Becker, J.H.A., Nilsson, G.E., 2005. Shrimps remove ectoparasites from fishes in temperate waters. *Biology Letters* 1: 454–456.

Page, T.J., Short, J.W., Humphrey, C.J., Hillyer, M.J., Hughes, J.M., 2008. Molecular systematics of the Kakaducarididae (Crustacea: Decapoda: Caridea). *Molecular Phylogenetics and Evolution* 46: 1003–1014.

Pereira, G., 1997. A cladistic analysis of the freshwater shrimps of the family Palaemonidae (Crustacea, Decapoda, Caridea). *Acta Biologica Venezuelica* 17(supl.1): 1–69.

Pereira, G., De Stefano, H., Staton, J., Farrell, B., 2002. Phylogenetic relationships in some species of the genus *Macrobrachium* based on nucleotide sequences of the mitochondrial gene cytochrome oxidase In: *Modern approaches to the study of Crustacea*, Escobar-Briones E. & Alvarez F. (ed.), 319–322.

Poore, G.C.B., 2016. The names of the higher taxa of Crustacea Decapoda. *Journal of Crustacean Biology* 36(2): 248–255.

Rohde, K., 2005. The nature of parasitism (chapter 1). In: Marine parasitology, K. Rohde (ed.), SCIRO Publishing, 565 pp.

Sazima, I., Grossman, A., Sazima, C., 2004. Hawksbill turtles visit moustached barbers: cleaning symbiosis between *Eretmochelys imbricata* and the shrimp *Stenopus hispidus*. *Biota Neotropica* 4(1): BN01504012004.

Short, J.W., Humphrey, C.L., Page, T.J., 2013. Systematic revision and reappraisal of the Kakaducarididae Bruce (Crustacea: Decapoda: Caridea) with the description of three new species of *Leptopalaemon* Bruce & Short. *Invertebrate Systematics* 27:87–117.

Schiaparelli, S., Ahyong, S.T., Bowden, D., 2015. Evidence of niche conservatism and host fidelity in the polar shrimp *Lebbeus* kiae n. sp.(Decapoda: Caridea: Thoridae) from the Ross Sea, Antarctica. *Hydrobiologia* 761(1): 45–69.

Schmitt, W.L., 1921. The marine decapod Crustacea of California. *University of California Publications in Zoology* 23: 1–470.

Stevens, B.G., Anderson, P.J., 2000. An association between the anemone, *Cribrinopsis fernaldi*, and shrimps of the families Hippolytidae and Pandalidae. *Journal of Northwest Atlantic Fishery Science* 27: 77–82.

Thiel, M., Baeza, J.A., 2001. Factors Affecting the Social Behaviour of Crustaceans Living Symbiotically with Other Marine Invertebrates: A modeling Approach. *Symbiosis* 30: 163–190.

Thompson, J.R., 1967. Comments on phylogeny of section Caridea (Decapoda: Natantia) and the phylogenetic importance of the Oplophoroidea. In: *Mar. Biol. Soc. India Symp. Crustacea*, Vol. 1, 314–326 pp.

Udekem d'Acoz, C. d', 2001. Description of *Gnathopylleptum tellei* gen. nov., sp. nov., a remarkable new gnathophyllid shrimp from Canary Islands (Crustacea, Decapoda, Caridea). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 71: 113–125.

Versluis, M., Schmitz, B., Heydt, A., Lohse, D., 2000. How snapping shrimp snap: through cavitating bubbles. *Science* 289: 2114–2117.

Wicksten, M.K., 2009. Interactions with fishes of five species of *Lysmata* (Decapoda, Caridea, Lysmatidae). *Crustaceana* 82: 1213–1223.

Wirtz, P., 1997. Crustacean symbionts of the sea anemone *Telmatactis cricoides* at Madeira and Canary Islands. *Journal of Zoology, London* 242: 799–811.

Wirtz, P., de Melo, G., De Grave, S., 2009. Symbioses of decapod crustaceans along the coast of Espírito Santo, Brazil. *Marine Biodiversity Records* 2: e162.

WoRMS Editorial Board, 2016. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2016-08-10

Yang, H.J., Ko, H.S., 2004. Zoeal stages of *Conchodytes nipponensis* (Decapoda: Palaemonidae) reared in the laboratory. *Journal of Crustacean Biology* 24: 110–120.